STUDIES IN NEOTROPICAL PALEOBOTANY. V. THE LOWER MIOCENE COMMUNITIES OF PANAMA— THE CULEBRA FORMATION[1]

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ABSTRACT

The lower Miocene Culebra Formation of central Panama consists of lignites and lignitic shales in a predominantly estuarian sandstone sequence. Forty-one palynomorphs have been identified from the lignites, and the following ten are most abundant: Monolete fern spore type 2 (20%), Manicaria-type palm pollen (10%), Cyathea (8%), Cryosophia-type palm pollen (8%), Selaginella (7%), Synechanthus-type palm pollen (6%), Rhizophora (6%), monolete fern spore type 1 (5%), Hampea/Hibiscus (4%), and Lycopodium (2%). Ferns constituted 25% of the fossil flora, palms 24%, and lowland vegetation types totaled 71%. The most prominent paleocommunities were the tropical moist forest represented by 30 genera that can occur in this vegetation type (including an only moderately developed mangrove swamp), premontane wet forest (25 genera), tropical wet forest (22 genera), and possibly some form of the premontane moist forest (12 genera). Communities of higher elevations and dry to arid habitats (including savannahs) were poorly represented to absent. Paleoenvironments were similar to those of the present, including annual rainfall estimated at about 275–325 cm (107–128 inches). The rainfall probably decreased slightly with elevation, similar to the pattern shown in a transect from sea level to about 1,172 m from present-day Atlantic Costa Rica (353.6–188.9 cm). Annual temperature probably ranged between about 21℃ and 32℃, as on adjacent Barro Colorado Island today. These estimates are consistent with the general paleotemperature curve derived from [18]O studies of marine invertebrates, and with emerging paleobotanical data from other Central America Tertiary floras. The geographic affinities of the Culebra flora are distinctly Central and North American, with all of the 41 taxa identified represented in the modern flora of Panama. Pollen of the Gramineae and shrubs of open, drier habitats continue to be rare or absent in Tertiary formations from southern Central America.

The geologic formations of central Panama provide an opportunity to trace vegetational and paleoenvironmental history through five segments of Tertiary time. The Gatuncillo Formation exposed near Alcalde Díaz is of middle(?) to late Eocene age, and study of this paleoflora has been completed (Graham, 1985). The Culebra, Cucaracha, and La Boca formations are of lower Miocene age, and the Gatun Formation is upper Miocene/Pliocene in age (a recent estimate by Vokes, pers. comm., 1988, is that the Gatun Formation may be as young as middle Pliocene). All are known to contain fossil pollen and spores. These studies, together with those of Bartlett & Barghoorn (1973) on Quaternary vegetation, and information on the modern vegetation (Croat, 1978; D'Arcy, 1987; the re-

cently completed *Flora of Panama*; and the Flora Mesoamericana project) will eventually provide a more complete data base for the vegetation of Panama and its Cenozoic evolution than for any other area in the Neotropics.

Concepts on the history of neotropical vegetation are being developed at a time when important new information is also becoming available on other aspects of the biotas. This allows comparison of the paleobotanical data with global paleotemperature and sea-level curves (Savin, 1977; Savin & Douglas, 1985; Savin et al., 1975; Vail & Hardenbol, 1979; Vail et al., 1977; Haq et al., 1987) and studies on marine invertebrates (Jones & Hasson, 1985) and terrestrial vertebrates (e.g., see papers in Stehli & Webb, 1985). This allows in-

terpretation within an increasingly precise paleo-physiographic context (Buskirk, 1985; Coney, 1982; Gose, 1985; Smith, 1985).

Other than a few megafossil studies done earlier in the century (see literature in Graham, 1973, 1979, 1982, 1986), the plant microfossils of the Culebra Formation provide only our second insight into lower Miocene vegetation of northern Latin America. The other is an assemblage from the lower Miocene Uscari sequence of Costa Rica (Graham, 1987a).

THE COLLECTING LOCALITY

The Culebra Formation belongs to a complex of lower Miocene strata in the Canal region of Panama (Graham et al., 1985: 489). Material was obtained from a well (Hole No. GH-9) drilled in January 1958 by the Panama Canal Commission. The site was near Gold Hill on the west side of the Canal at latitude 9°02′N, longitude 79°38′W. Fifty-seven samples were taken from lignites or lignitic shales along the 154-m core between levels 491.6 and 377, and 21 yielded pollen and spores. Eleven were selected for study from the following depths (in feet, following the original log data): 377, 407, 415.5, 425, 456, 469.8, 470.6, 488, 490.6, 491, and 491.6.

The 57 samples totaled approximately 9.5 feet of coalified lignite and lignitic shale (avg. ca. 2 inches/sample), with numerous narrow bands adding another ca. 1.5 feet (9.6%). The rest of the core was mostly sandstone (Graham et al., 1985: 489–491, tables 1, 2), and constituted ca. 103 feet (90.4%). Swift (1977) has studied Holocene sedimentation rates in the Panama Basin, but there have been no studies on the Culebra or other Tertiary formations. In general, near-shore sandstones and lignites deposited in an estuarian environment in tectonically active regions accumulate rapidly. In the absence of more precise data, the time span represented by the section is estimated at a few to several tens of thousands of years. Other details on the geology of the Culebra and related formations are given in Graham et al. (1985).

MATERIALS AND METHODS

Extraction and processing techniques are described in Graham (1985). Slides are labeled Pan Core, Culebra, with depth and slide number cited. Location of specimens on the slides is by England Slide Finder coordinates (e.g., ESF L-39, 1). All materials are deposited in the palynology collections at Kent State University.

SYSTEMATICS

Forty-one palynomorphs were identified from the Culebra Formation, and a number of others were recovered whose biological affinities could not be established. Some of the more distinctive and/or common ones are listed as Unknown types 1–14 in Table 1. Further details of the identification procedures are given in Graham (1985: 507–508).

LYCOPODIACEAE

Lycopodium (Figs. 1–3). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, ca. 20 μm long, extending to and occasionally branching at spore margin, inner margin entire; distal surface with numerous circular punctae ca. 1 μm diam., proximal surface laevigate; wall ca. 1.5–2 μm thick; 35–37 μm.

These spores are similar to the modern *L. reflexum* Lam./*L. linifolium* L. type (cf. Tryon & Tryon, 1982: 811, fig. 22), presently growing in moist shaded habitats in Panama. Similar spores have been reported from the lower Miocene Uscari shale sequence in Costa Rica (Graham, 1987a).

SELAGINELLACEAE

Selaginella (Fig. 4). Spherical to nearly bilateral, amb circular to reniform; trilete, laesurae frequently obscured by wall thickness and sculpture elements, straight, narrow, ca. 20–22 μm long, extending nearly to spore margin, inner margin entire; echinate, echinae short (ca. 2 μm), occasionally curved, dense, bases broad; wall ca. 2 μm thick (excluding echinae); 26–30 μm.

Microspores of *Selaginella* vary in size, and specimens from the Culebra Formation are relatively small (26–30 μm) and thick-walled. They are common in the Gulf/Caribbean Tertiary and have been reported from all formations studied in the present project (Eocene Gatuncillo Formation of Panama, Graham, 1985; Oligocene San Sebastian Formation of Puerto Rico, Graham & Jarzen, 1969; lower Miocene Uscari sequence of Costa Rica, Graham, 1987a; lower Miocene Culebra Formation of Panama, present report; and upper Miocene Paraje Solo Formation of Veracruz, Mexico, Graham, 1976). *Selaginella* is widely distributed in tropical regions in shaded, humid habitats.

CYATHEACEAE

Cyathea (Figs. 7–9). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, 14–16 μm long, extending to spore margin, inner

TABLE 1. *Identification and numerical representation of fossil palynomorphs from the lower Miocene Culebra Formation, Panama. Figures are percentages based on counts of 200, except levels 377–425, which are based on 100 due to lower concentration and only fair preservation of the specimens; these levels also contain high percentages of fungal spores.*

	491.6	491	490.6	488	470.6	469.8	456	425	415.5	407	377
Lycopodiaceae											
Lycopodium	12	1	—	—	3.5	—	—	3	4	—	—
Selaginellaceae											
Selaginella	13	5	6.5	6.5	7	9	2	12	10	5	3
Cyatheaceae											
Cyathea	9	9.5	12	7.5	5.5	7	7.5	5	8	—	—
Pteridaceae											
Pteris	—	—	—	2	--	—	1.5	—	—	—	—
Schizaeaceae											
Lygodium	—	—	2	3.5	—	—	1	—	—	—	—
Vittariaceae											
cf. *Antrophyum*	2	1.5	2	2	2	—	1	—	—	—	—
Trilete fern spores											
Type 1	—	—	1	—	1.5	—	—	—	1	—	—
Type 2	3	—	2	—	1.5	0.5	1	—	—	—	—
Type 3	—	—	—	—	2	—	2	—	—	—	—
Type 4	—	—	—	—	1	—	—	—	—	—	—
Marattiaceae											
Danaea	—	—	—	—	0.5	—	1	—	—	—	—
Monolete fern spores											
Type 1	9.5	8	5	8.5	2.5		5	4	1	2	—
Type 2	15.5	37	28	15.5	12.5	19	12.5	24	12	32	20
Type 3	—	—	—	—	—	0.5	1	—	—	—	—
Gramineae	—	—	0.5	—	—	—	0.5	—	—	1	—
Palmae											
Cryosophila-type	7.5	4.5	7.5	5	8.5	9	10	13	10	8	5
Desmoncus-type	—	—	—	1	0.5	—	—	—	—	—	—
Manicaria-type	—	8.5	7.5	10	5	22	7.5	10	15	15	15
Synechanthus-type	5.5	10.5	2.5	4.5	2		1.5	12	11	3	30
Aquifoliaceae											
Ilex	—	—	—	0.5	2.5	0.5	2.5	—	1	—	—
Chenopodiaceae/											
Amaranthaceae	—	—	—	—	1	—	—	—	—	—	—
Combretaceae											
Combretum/Terminalia	—	—	—	0.5	3	—	1	—	—	—	—
Compositae	—	—	—	0.5	—	—	—	—	—	—	—
Connaraceae											
cf. *Rourea*	—	—	—	—	1.5	0.5	1	—	—	—	—
Dilleniaceae											
cf. *Doliocarpus*	—	—	—	—	—	0.5	0.5	—	—	—	—
Dioscoreaceae											
Dioscorea/Rajania	—	—	—	—	0.5	—	—	—	—	—	—

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TABLE 1. *Continued.*

	491.6	491	490.6	488	470.6	469.8	456	425	415.5	407	377
Euphorbiaceae											
Alchornea	—	—	—	—	—	1.5	0.5	—	—	—	—
Sapium	—	—	—	—	—	—	2.5	—	—	—	—
Tetrorchidium	—	—	—	1	1.5	—	1.5	—	—	1	—
Flacourtiaceae											
Casearia	—	—	—	—	1.5	—	—	—	—	—	—
Leguminosae											
Mimosoideae											
Acacia	—	—	—	0.5	—	—	0.5	—	—	—	—
Malpighiaceae	—	—	—	2	1	—	—	—	1	—	—
Malvaceae											
Hampea/Hibiscus	7.5	4	4.5	4	3.5	5	1	2	1	3	3
Myrtaceae											
Eugenia/Myrcia	—	—	—	0.5	1.5	—	—	—	—	—	—
Rhizophoraceae											
Rhizophora	10.5	4	3.5	8.5	5.5	1.5	2.5	5	9	8	6
Rubiaceae											
Sabicea	—	—	—	—	—	—	0.5	—	—	—	—
Sapindaceae											
Allophylus	—	—	1	—	—	1	0.5	—	—	—	—
Cupania	0.5	—	—	—	—	—	0.5	—	—	—	—
Matayba	0.5	—	—	—	0.5	—	—	—	—	—	—
Sapotaceae											
cf. *Pouteria*	—	—	—	—	0.5	—	—	—	—	—	—
Sterculiaceae											
cf. *Guazuma*	—	—	—	—	—	—	0.5	—	—	—	—
Unknown											
Type 1	—	—	—	—	0.5	—	—	1	—	—	—
Type 2	—	—	0.5	—	—	—	1	—	—	—	—
Type 3	—	0.5	4.5	4.5	6	11.5	7.5	2	—	4	4
Type 4	—	—	—	0.5	—	—	—	—	—	—	—
Type 5	—	—	—	—	1.5	—	2	—	—	—	—
Type 6	—	—	—	—	—	—	0.5	—	—	—	—
Type 7	—	—	—	—	—	0.5	—	—	—	—	—
Type 8	—	—	—	0.5	—	—	1.5	—	—	—	—
Type 9	—	—	—	—	—	—	0.5	—	—	—	—
Type 10	—	—	—	0.5	—	1	1.5	—	—	—	—
Type 11	—	—	0.5	2	1.5	0.5	3.5	1	2	—	—
Type 12	—	—	—	—	—	—	0.5	—	—	—	—
Type 13	—	—	—	—	1	—	1.5	—	—	—	—
Type 14	—	—	—	1	1.5	1	1.5	—	—	—	—
Other unknowns	4	6	9	7	7	8	8	6	14	18	14

margin entire, bordered by lip 2–3 μm wide with punctae 1 μm diam.; distal surface finely punctate, proximal surface more laevigate near laesurae; wall 1.5–2 μm thick; 32–36 μm.

The classification of tree ferns differs among various authors, and reference slides with spores similar to the fossil specimens come from herbarium material labeled as *Alsophila* and *Cyathea*. As

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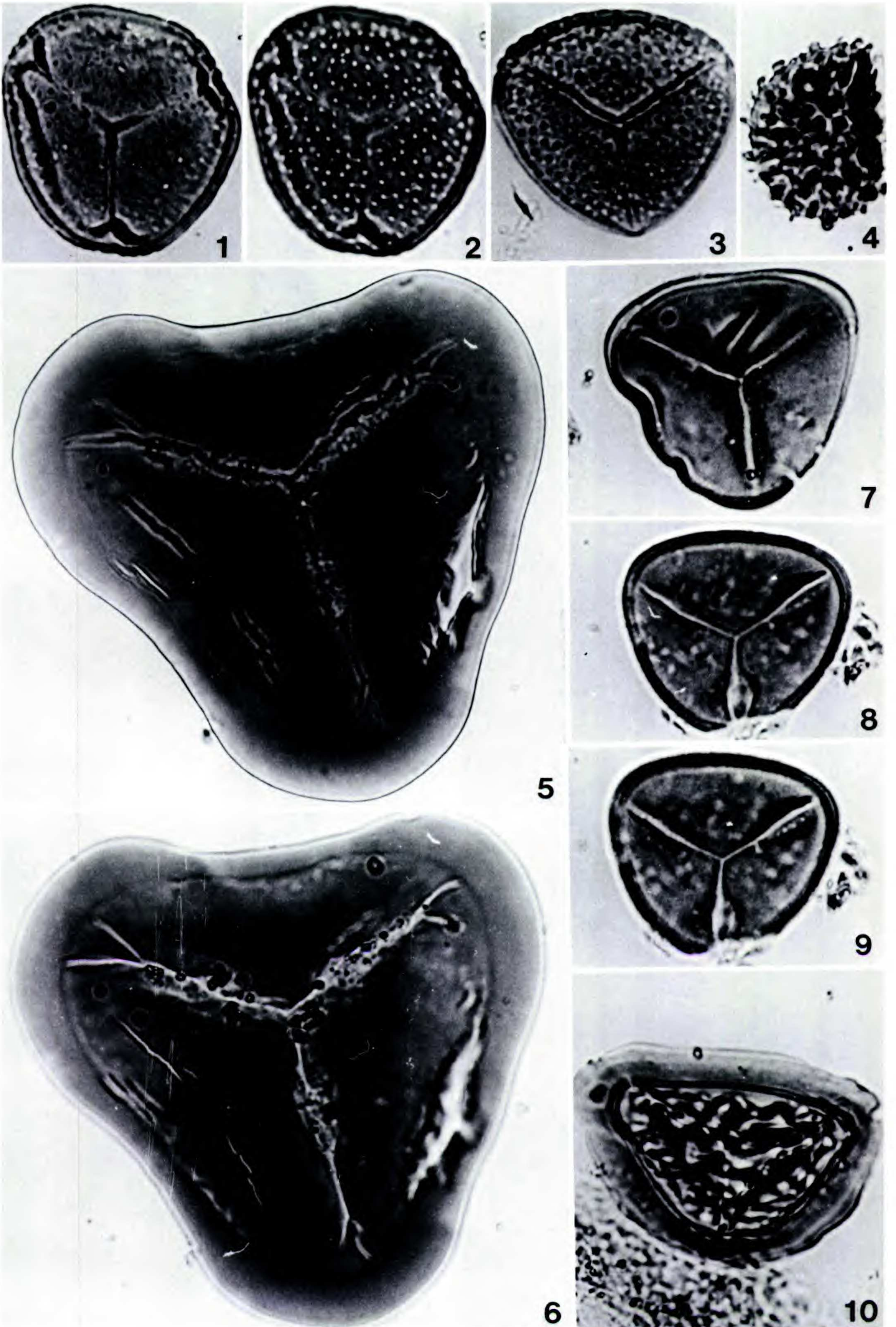
noted by Tryon & Tryon (1982: 204), "The name *Cyathea* has been variously applied to genera of widely different scope and definition, sometimes including nearly all members of the family." In illustrations of spores of neotropical tree ferns (Gastony & Tryon, 1976; Tryon & Tryon, 1982: 207), the micropunctate forms are referred to *Cyathea*.

The genus consists of 40 species of the American tropics growing primarily in montane forests and cloud forests, and also in low rain forests in Central America, usually at 1,500–2,000 m, but as low as 500 m (Tryon & Tryon, 1982: 204–205). Fossil spores are common in Gulf/Caribbean Tertiary deposits.

PTERIDACEAE

Pteris (Fig. 10). Amb triangular, apices rounded; trilete, laesurae straight, narrow, 18–22 μm long, extending to spore margin, inner margin entire; distal surface with coarse, irregular verrucae, proximal surface more laevigate, flange ca. 5–6 μm wide, hyaline; wall 2 μm thick; 42–48 μm.

Pteris includes about 200 species, with approximately 55 occurring in the American tropics (Tryon & Tryon, 1982: 334). The plants typically grow in wet forests or in openings along stream banks at low elevations (sea level to 2,000 m). Fossil spores are frequent, but in low percentages in Gulf/Caribbean Tertiary deposits.

SCHIZAEACEAE

Lygodium (Figs. 5, 6, 11, 12, 17). Amb triangular to concavo-triangular, apices rounded; trilete, laesurae ± straight, narrow, 34–38 μm long, extending nearly to spore margin, apices frequently branched, inner margin entire; laevigate to faintly verrucate; wall 2–4 μm thick; 80–100 μm.

Lygodium is a genus of about 30 species, with six to eight in the American tropics. According to Tryon & Tryon (1982: 71): "*Lygodium* characteristically occurs in open forest especially along the borders where the climbing leaves can reach well-lighted situations. In tropical America, it sometimes grows in rain forests, but more commonly in gallery forests, shrubby savannahs or along the borders of streams or river banks. It most commonly occurs from sea level to about 350 m, as a characteristic element of the low, humid tropics, and less often grows up to 1,000 m."

The specimens are large (up to 100 μm in diameter) and somewhat diverse in morphology; more than one biological species may be represented. The most notable variation is in the dark coloration that can occur at the apices. This is not found in our modern reference material, but in the fossil specimens it ranges from absent (Figs. 5, 6) to quite prominent (Fig. 17). Spores of *Lygodium*, but of a different morphological type, have been reported from the upper part of the lower Miocene in northern South America (Germeraad et al., 1968) under the artificial generic name *Crassoretitriletes*. Spores similar to the Culebra specimens are also known under the name *Matonisporites* described by Couper (1958; see especially pl. 20, figs. 15, 16) from the Jurassic and Lower Cretaceous of England. Dettmann (1963, pl. 11, figs. 1, 2) emended the description to include the thickened apices and reported the genus from Lower Cretaceous deposits of southeastern Australia. She noted (p. 59) possible affinities with *Dicksonia* (*D. sellowiana* Hook., *D. antarctica* Labill.), but our modern reference material of these species, and others in the genus, is different (see illustrations in Tryon & Tryon, 1982: 148). Recently Jameossanaie (1987, fig. 10, #5) described similar spores (*Matonisporites*) from the Upper Cretaceous of New Mexico. The Culebra specimens are the first of the type illustrated in Figures 5, 6, 11, 12, and 17 for the Gulf/Caribbean region.

VITTARIACEAE

Cf. *Antrophyum* (Figs. 18, 20). Amb triangular, apices rounded; trilete, laesurae relatively small in relation to spore diameter, straight, narrow, 10–14 μm long, extending ca. ⅔ distance to spore margin, inner margin entire; laevigate; wall ca. 1.5 μm thick; 52–65 μm.

Approximately ten of the ca. 40 species of *Antrophyum* occur in the Neotropics from Hidalgo, Mexico, through Central America and the Antilles,

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FIGURES 1–10. *Fossil spores from the Culebra Formation, Panama. 1–3. Lycopodium.—1, 2. Pan core 470.6, slide 3a, ESF L-39, 1.—3. Pan core 470.6, slide 3a, ESF W-31, 2.—4. Selaginella. Pan core 470.6, slide 3a, ESF K-28, 1.—5, 6. Lygodium. Pan core 488, slide 1, ESF Q-32, 4. 7–9. Cyathea.—7. Pan core 456, slide 3, ESF M-16, 1–2.—8, 9. Pan core 456, slide 3, ESF B-13, 304.—10. Pteris. Pan core 488, slide 1, ESF D-18, 3.*
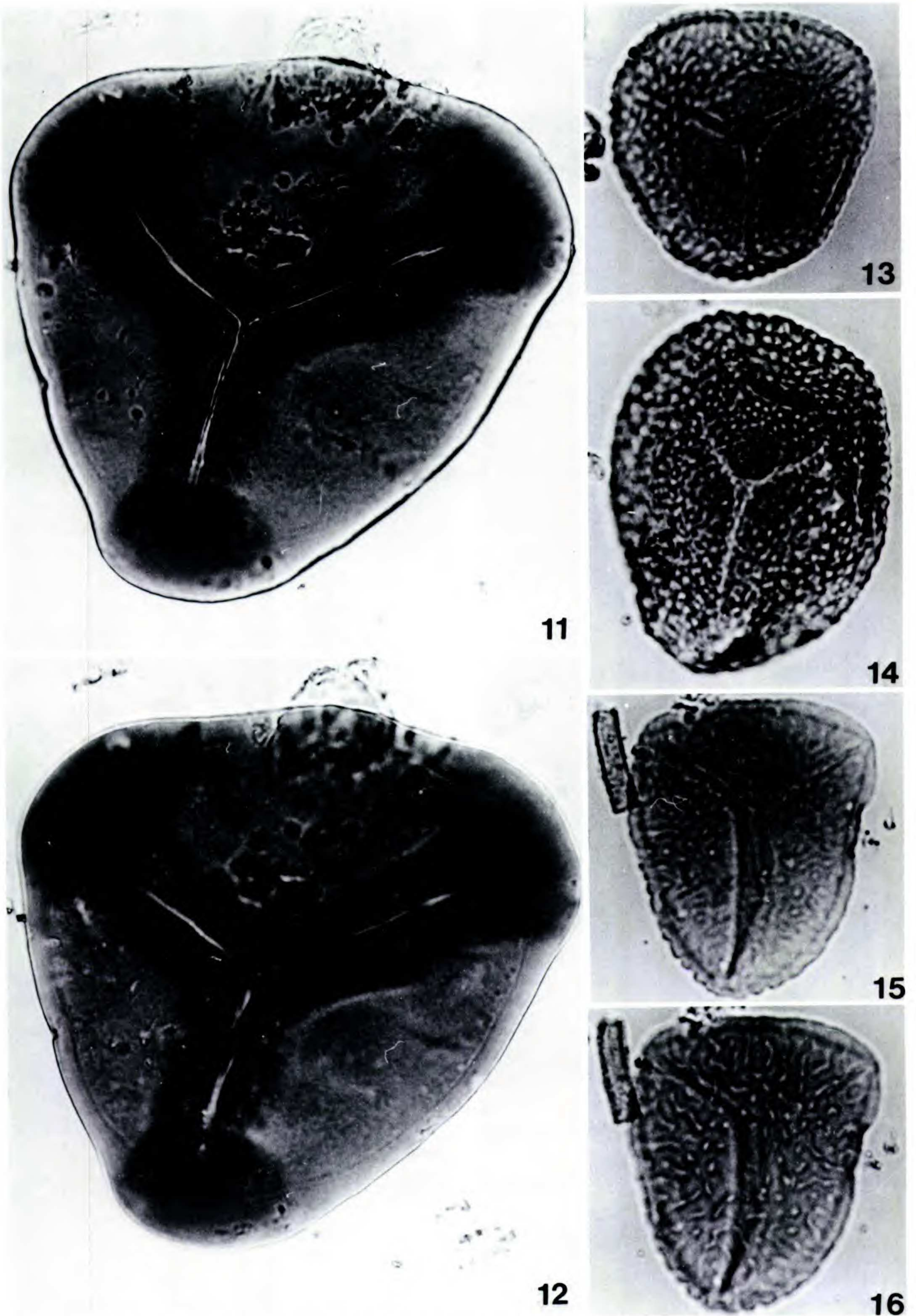
FIGURES 11–16. *Fossil spores from the Culebra Formation, Panama.*—*11, 12. Lygodium. Pan core 488, slide 1, ESF L-14.*—*13. Trilete fern spore type 1. Pan core 490.6, slide 1, ESF H-36, 1.*—*14. Trilete fern spore type 2. Pan core 456, slide 4, ESF F-22, 3.*—*15, 16. Trilete fern spore type 3. Pan core 470.6, slide 2a, ESF E-35, 1–2.*

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to northern Argentina and southeastern Brazil. The genus grows in rain forests and cloud forests, usually at elevations of 100–1,500 m. The specimens are laevigate, while modern spores often have a delicate sculpture ("echinate rods and surface strands," Tryon & Tryon, 1982: 360–361). Tryon & Tryon believe, however, that a perispore is present, and in fossil specimens this ornamental covering would not be preserved. Similar large, trilete, laevigate spores are known from the Eocene of Panama (Graham, 1985, figs. 13, 16) and the Miocene of Veracruz, Mexico (Graham, 1976, fig. 227).

OTHER TRILETE FERN SPORES

Several trilete fern spores were recovered for which biological affinities could not be determined. Four of the more distinctive ones are described below.

Type 1 (Fig. 13). Amb oval-triangular; trilete, laesurae straight, narrow, ca. 20 μm long, extending to spore margin, inner margin ± entire; finely reticulate to micropunctate (width of muri equals diameter of lumen, ca. 1 μm), sculpture less dense near laesurae; wall ca. 1.5 μm thick; 42 μm.

Type 2 (Fig. 14). Amb oval-triangular to ± circular; trilete, laesurae straight, narrow, 20–22 μm long, extending ca. ⅔ distance to spore margin, inner margin entire; finely reticulate; wall 1.5 μm thick; 45–55 μm.

Type 3 (Figs. 15, 16). Amb oval-triangular to wedge-shaped, apices rounded; trilete, laesurae straight, narrow, 22–26 μm long, extending to spore margin, inner margin entire; punctate, punctae circular (ca. 1 μm) to elongated (2–4 μm) and slitlike and sinuous; wall 2 μm thick; 42 × 36 μm (slightly compressed).

Type 4 (Fig. 19). Amb irregular, ± oval-triangular, apices rounded; trilete, laesurae straight, narrow, 34–36 μm long, extending to spore margin, inner margin entire, conspicuous lip 12 μm wide (maximum, conspicuousness augmented by folds?); low, moundlike verrucae ca. 2–3 μm diam.; wall ca. 3 μm thick; 72 × 64 μm (compressed).

MARATTIACEAE

Danaea (Fig. 21). Amb circular to ± reniform; monolete, laesurae straight, narrow, 18–20 μm long, extending nearly to spore margin, inner margin entire; echinate, echinae ca. 2 μm long, relatively dense; wall 1 μm thick; 28–32 μm (excluding spines).

Danaea is a neotropical genus of about 20 species, which presently grows from southern Mexico, through Central America and the Antilles, into Venezuela, the Guianas, Bolivia, and the Amazon Basin (Tryon & Tryon, 1982: 47). It grows in moist habitats, wet forests, and rain forests from sea level to about 2,300 m. Fossil spores have not been reported previously from Tertiary deposits in the Gulf/Caribbean region.

OTHER MONOLETE FERN SPORES

Type 1 (Fig. 22). Reniform; monolete, laesura straight, narrow, 22–26 μm long, extending ca. ¾ spore length, inner margin entire; laevigate; 41 × 22 μm.

These spores likely represent the Blechnaceae (e.g., *Blechnum*) and Polypodiaceae (e.g., *Asplenium*, *Thelypteris*) without the delicate ornamented perispore. They are common in fossil deposits, recognized under the artificial generic name *Laevigatisporites*, and range from Paleozoic to Recent.

Type 2 (Fig. 23). Reniform; monolete, laesura straight, narrow, 22–26 μm long, extending ¾ spore length, inner margin entire; verrucate, verrucae moderately low and conspicuous, shape irregular, ca. 2 × 4 μm; wall 2–3 μm thick; 56–58 × 39–41 μm.

These spores are produced by species of several genera of the Polypodiaceae and Blechnaceae (e.g., *Blechnum*, *Microgramma*), bear the artificial generic name *Verrucatisporites*, and range from the Paleozoic to Recent.

Type 3 (Figs. 24–26). Reniform; monolete, laesura straight to curved, narrow, 32–36 μm long, extending ca. ½–⅔ spore length, inner margin entire; verrucate, verrucae distinct peglike structures, apices often flat, moderately to sparsely dense, ca. 2–3 μm diam.; 52–65 × 27–51 μm.

GRAMINEAE

(Fig. 27). Spherical, amb circular; monoporate, pore circular, 3 μm diam., inner margin entire, annulus ca. 2 μm wide, outer margin entire; tectate, wall ca. 2 μm thick; scabrate; 36–40 μm.

The Gramineae are stenopalynous, and the specimens cannot be referred to any single genus. Grass pollen has been reported from the Miocene of Veracruz (Graham, 1976) but not from the Eocene Gatuncillo Formation of Panama (Graham, 1985) or the lower Miocene Uscari sequence of Costa Rica (Graham, 1987a). Germeraad et al. (1968) listed its range in the Gulf/Caribbean region as base of the middle Eocene to Recent, but Muller
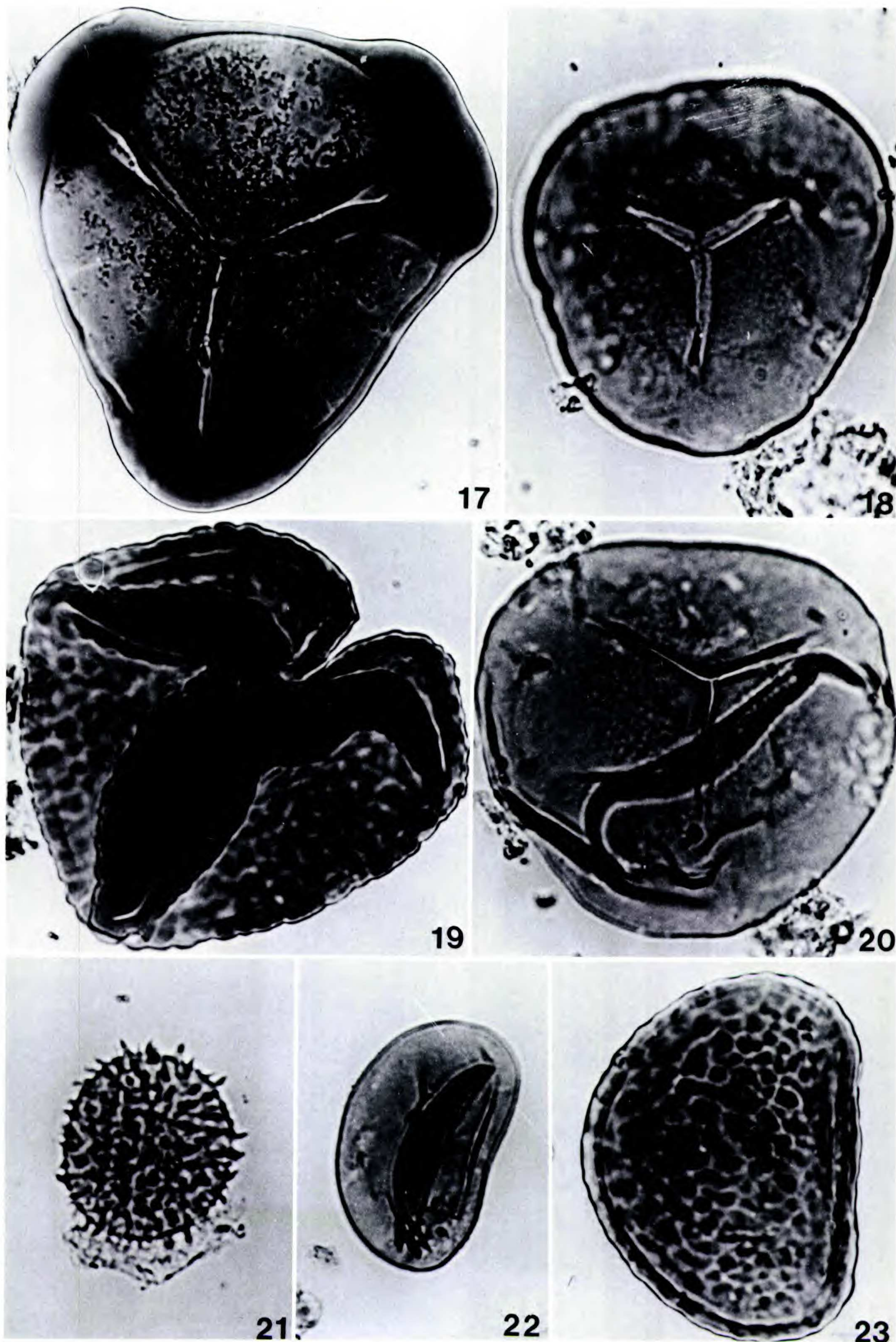
FIGURES 17–23.   *Fossil spores from the Culebra Formation, Panama.—17.* Lygodium. *Pan core 456, slide 4, ESF K-11, 2. 18, 20.* Cf. Antrophyum.—*18. Pan core 456, slide 1, ESF U-14, 3–4.—20. Pan core 456, slide*

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(1981) cited reports extending it back into the Paleocene of Brazil.

PALMAE

Palm pollen is one of the most common plant microfossils in the Culebra Formation. Four types are described, and it is likely that more than one genus may be represented by each.

Cryosophila-type (Figs. 29–32).   Prolate, amb oval; monocolpate, colpus straight, 24–26 μm long, extending entire length of grain, margin entire; tectate-perforate, wall 2 μm thick; reticulate, muri relatively broad (ca. 1–1.5 μm), flat, lumen ca. 2 μm diam. on distal side, smaller approaching colpus; 34–38 × 24–32 μm.

This is one of the most common types of palm pollen in the Culebra Formation (Table 1). It is very similar to that of *Cryosophila warscewiczii* (H. Wendl.) Bartl., a tree up to 10 m tall distributed from Belize to Panama. In Panama it is known from the "tropical moist forest on both slopes of the Canal Zone and in Panamá and Darién; known also from premontane wet forest in Coclé (El Valle) and Panamá (Cerro Campana) and from tropical wet forest in Darién" (Croat, 1978: 171). Palm pollen is usually abundant in Gulf/Caribbean Tertiary deposits, but this is the first report of the *Cryosophila* type. Bartlett & Barghoorn (1973: 230, figs. 5, 6) reported a more finely reticulate form from the Quaternary of Panama.

Desmoncus-type (Figs. 33, 34).   Prolate; monocolpate, colpus straight, broad, boatlike, apices rounded, 26–28 μm long, extending nearly entire length of grain, inner margin entire; tectate-perforate, wall ca. 1.5 μm thick; finely reticulate (diameter of lumen ca. 1 μm or slightly less); 30 × 18 μm.

This kind of pollen is produced by several palms, and *Desmoncus* is used primarily as an example of a morphologically similar type. A climbing palm known from Mexico to South America, it grows in Panama in tropical moist forests in the Canal region, in the provinces of Panamá and Darién, and in the tropical wet forest in Colón (Croat, 1978: 171).

Manicaria-type (Figs. 37, 38).   Prolate;

monocolpate, colpus straight to occasionally bent, 36–40 μm long, extending nearly entire length of grain, inner margin entire; finely reticulate (diameter of lumen ca. 1 μm or slightly less); tectate-perforate, wall ca. 1 μm thick; 40–45 × 21–27 μm, widest part just off equator of grain.

Manicaria is used as an example of a palm producing pollen morphologically similar to the specimens. It is a tree up to 10 m tall with three species in the Antilles, Central America, and South America (fide Bailey, 1943) and often occurs in dense groves in wet places. Similar pollen of this general palm type has been reported from the Eocene of Panama (Graham, 1985, fig. 26).

Synechanthus-type (Figs. 35, 36).   Prolate; monocolpate, colpus straight, 28–30 μm long, extending entire length of grain, inner margin entire; scabrate (to possibly microreticulate); tectate, wall 1.5–2 μm thick; 28–34 × 22–26 μm.

Synechanthus is representative of modern palms producing morphologically similar pollen (cf. also *Aiphanes*, the West Indian *Thrinax*). It is a tree to 6 m tall distributed from Costa Rica to Colombia and Ecuador, usually at low elevations. In Panama it is known from "tropical moist forest on both slopes in the Canal Zone and in San Blas and Darién, from premontane wet forest in Veraguas (Cerro Tute) and Panamá (Lago Cerro Azul), and from premontane rain forest in Panama (Cerro Jefe) and Darién (Cerro Pirre)" (Croat, 1978: 178).

AQUIFOLIACEAE

Ilex (Fig. 28).   Oblate-spheroidal, amb circular; tricolporoidate, colpi straight, 9–11 μm long (pole to equator), tapering to acute apex, equatorially arranged, meridionally elongated, equidistant, extending within 7 μm of pole (P.I. 0.33), inner margin diffuse, pores obscure, diam. ca. 2–3 μm, circular, situated at midpoint of colpus; intectate, clavate, wall 3 μm thick; 25–30 μm.

Ilex is one of the most common microfossils in the Gulf/Caribbean Tertiary, and its stratigraphic range and ecology have been discussed previously (e.g., Graham, 1985: 514). Briefly, its geologic range is from Late Cretaceous to Recent (Muller, 1981), and in northern Latin America pollen has been recovered from all formations studied in the

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4, ESF J-27.—19. Trilete fern spore type 4. Pan core 470.6, slide 2a, ESF K-34, 1.—21. Danaea. Pan core 456, slide 3, ESF K-7, 2.—22. Monolete fern spore type 1. Pan core 470.6, slide 2a, ESF T-31, 2.—23. Monolete fern spore type 2. Pan core 470.6, slide 2a, ESF S-28, 2-4.
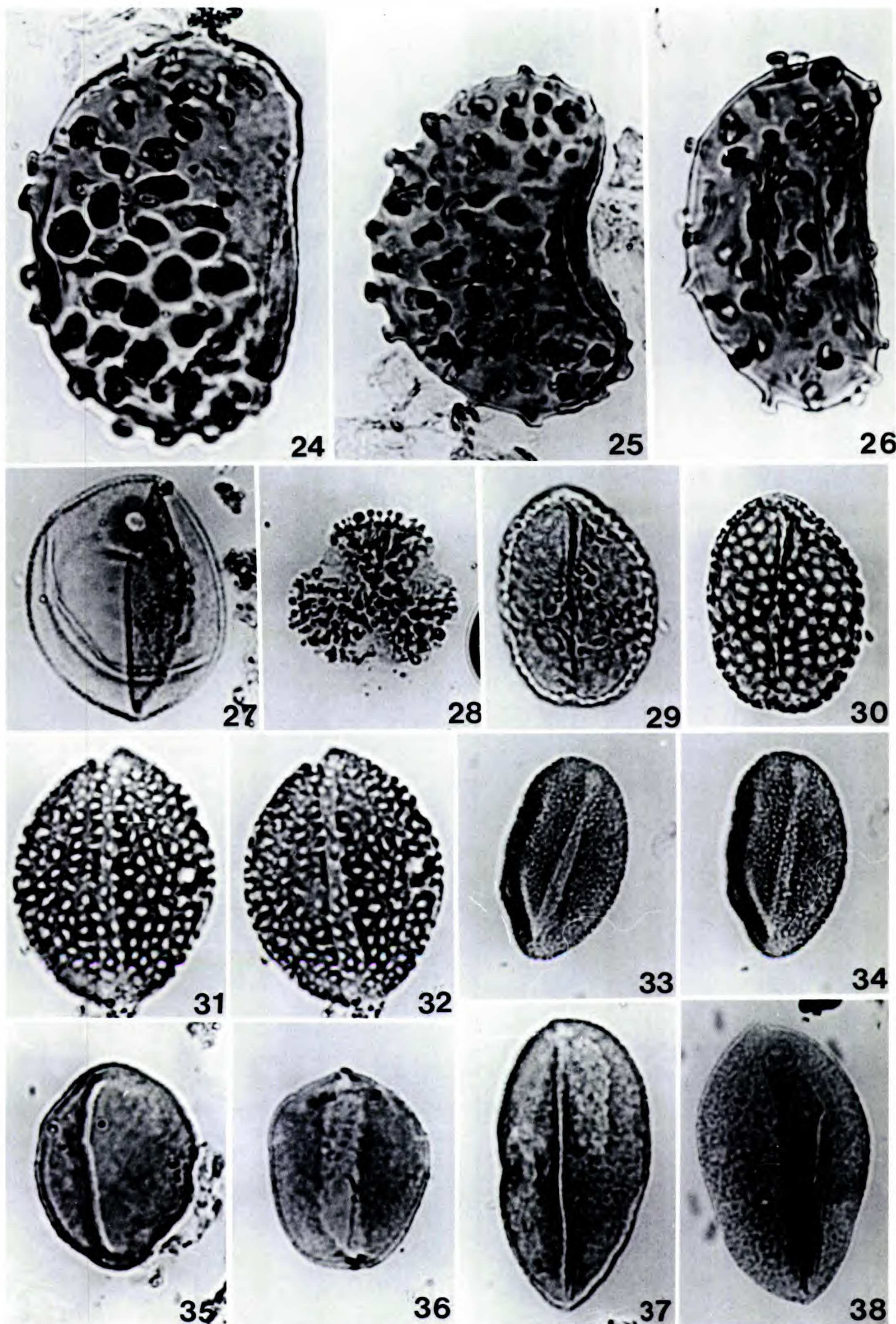
FIGURES 24-38. *Fossil spores and pollen from the Culebra Formation, Panama.—24-26. Monolete fern spore type 3. Pan core 456, slide 1, ESF R-25, 1-3; Pan core 470.6, slide 2a, ESF L-18; Pan core 470.6, slide 2a,*

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present project (Eocene to Recent). In the modern flora it grows at mid altitudes in moist to slightly drier habitats.

CHENOPODIACEAE/AMARANTHACEAE

(Fig. 39). Spherical, amb circular; periporate, pores circular, evenly distributed, distance between pores ca. 6–8 μm, estimated number ca. 40, diam. 3 μm, inner margin entire; tectate, wall relatively thick (3 μm); psilate; 21–23 μm.

Pollen of genera in these two families cannot be distinguished consistently, and the specimens serve only to record the family (or families) in the lower Miocene vegetation of Panama.

COMBRETACEAE

Combretum/Terminalia (Figs. 40, 41). Prolate to prolate-spheroidal; tricolporate with 3 pseudocolpi, colpi straight, 15 μm long, apices blunt, equatorially arranged, meridionally elongated, equidistant, inner margin entire, pore frequently obscure, circular, diam. 2–3 μm, situated at midpoint of colpus; tectate, wall 1.5–2 μm thick; psilate to faintly scabrate; 14–16 × 18–20 μm.

The occurrence of *Combretum/Terminalia* in Gulf/Caribbean deposits has been discussed recently by Graham (1985). Pollen of the two genera cannot be distinguished consistently (Graham, 1980), and the morphological type ranges from Eocene to Recent in the region. Both genera are found in moist to wet habitats, although individual species may range into drier habitats.

COMPOSITAE

(Figs. 42, 43). Spherical to oblate-spheroidal, amb circular; tricolporate, colpi straight, short (ca. 4–6 μm pole to equator), equatorially arranged, meridionally elongated, equidistant, pore obscure, ca. 2 μm diam., situated at midpoint of colpus; vesiculate (air cavities evident in equatorial mesocolpial region); tectate, outer wall 3–4 μm thick; echinate, spines short (ca. 3 μm), base broad, moderately dense (distance between spines ca. 3–4 μm); 24–26 μm.

These vesiculate Compositae pollen grains are typical of later Cenozoic deposits and have not been reported previously in our studies, although other Compositae pollen types are known from the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976). The Culebra specimens are of the Heliantheae type (e.g., *Ambrosia, Franseria, Iva*) but cannot be referred to any one genus.

CONNARACEAE

Cf. *Rourea* (Figs. 44, 45). Prolate; tricolpate, colpi straight, 16–18 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire to appearing minutely dentate due to overlying sculpture elements; tectate, wall ca. 1 μm thick; finely reticulate; 20–24 × 14–18 μm.

These prolate, tricolpate reticulate grains are a generalized type but compare most closely to members of the Connaraceae, especially *Rourea*. The genus is represented in Panama by three species (fide Woodson & Schery, 1950a), the most common being *R. glabra* Aubl., distributed from southern Mexico, through Central America and the Antilles, to the Guianas and Brazil. In Panama it is "known principally from tropical moist forest in the Canal Zone, San Blas, Veraguas, Los Santos, Panamá, and Darién; known also from tropical dry forest in Coclé and Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Colón and Panamá" (Croat, 1978: 423).
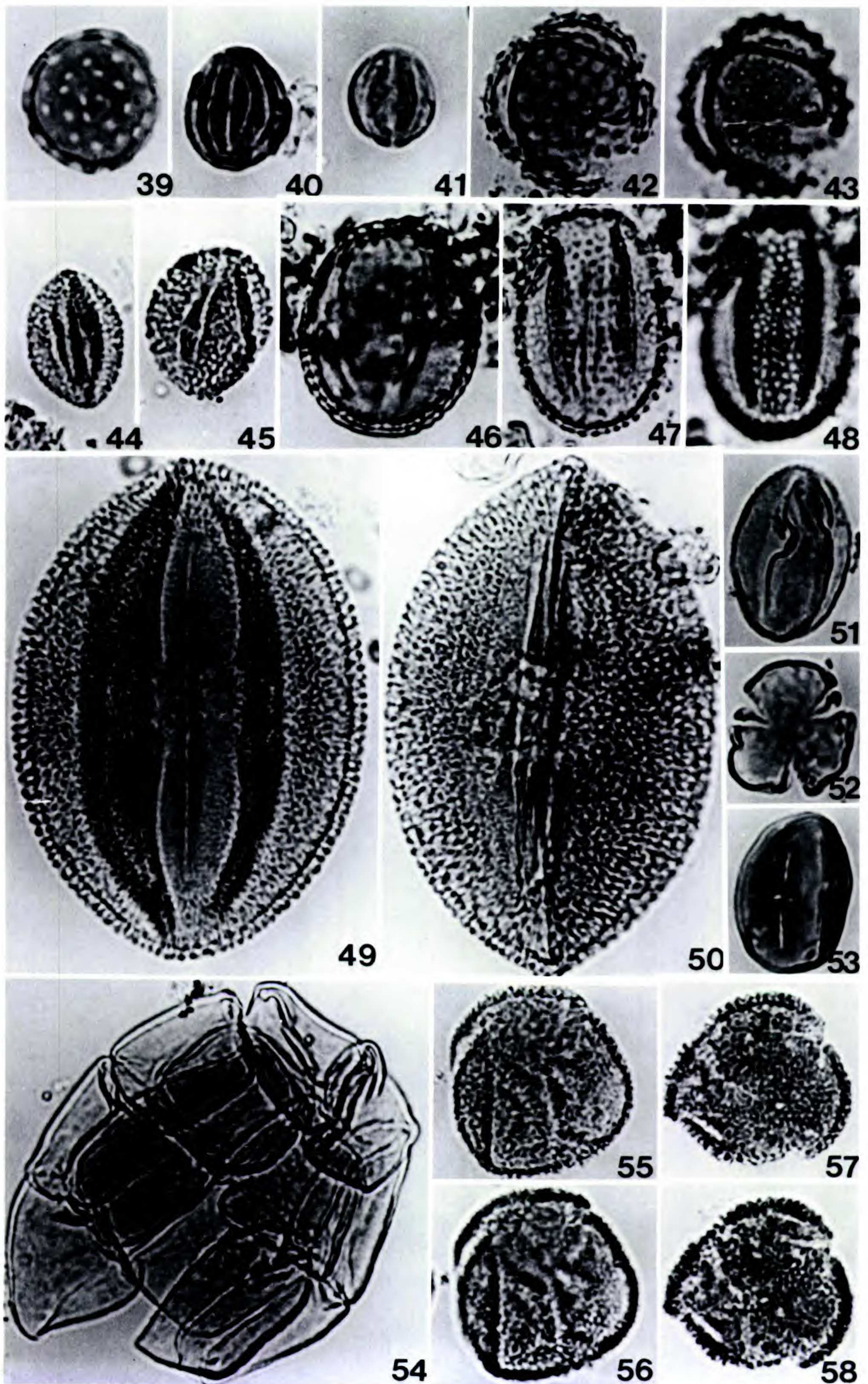
DILLENIACEAE

Cf. *Doliocarpus* (Figs. 46–48). Prolate to prolate-spheroidal; tricolporate, colpi straight, 23–25 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 3 μm wide, pore obscure, circular, ca. 3 μm diam., situated at midpoint of colpus; tectate perforate, wall 2.5–3 μm thick; reticulate, muri smooth, about as wide as lumen; 30–34 × 20–24 μm.

Four species of *Doliocarpus* presently occur in the vicinity of the collecting site: *D. dentatus* (Aubl.) Standley, *D. major* J. F. Gmel., *D. multiflorus* Standley, and *D. olivaceus* Sprague & L. O. Williams ex Standley. The specimens are most similar to *D. dentatus*, but there is some variation in the

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ESF R-22, 1.—27. *Gramineae. Pan core 456, slide 4, ESF N-9, 3–4.*—28. Ilex. *Pan core 488, slide 1, ESF S-9, 1–2.*—29–32. Cryosophila-*type. Pan core 488, slide 1, ESF S-10, 2–4; Pan core 456, slide 3, ESF V-10, 1.*—33, 34. Desmoncus-*type. Pan core 470.6, slide 3a, ESF J-24.*—35, 36. Synechanthus-*type. Pan core 456, slide 1, ESF U-35, 2–4; Pan core 469.8, slide 2, ESF U-16, 3.*—37, 38. Manicaria-*type, Pan core 456, slide 3, ESF S-12, 1; Pan core 470.6, slide 3a, ESF N-27, 3–4.*

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modern pollen among individual herbarium collections. In the collection *Lewis et al. 722A* (Chiriquí, Panama, MO) the reticulum is slightly coarser (muri broader) like the specimens, while in the collection *Proctor et al. 27037* (Nicaragua, CR) the reticulum is finer. Consequently the fossil specimens are presently identified only as cf. *Doliocarpus*.

Doliocarpus dentatus occurs from Mexico through Central America to Paraguay and is scattered in the Antilles. In Panama it grows in the tropical moist forest, tropical dry forest, premontane moist forest, and premontane wet forest (Croat, 1978: 599).

DIOSCOREACEAE

Dioscorea/Rajania-type (Fig. 51). Prolate; tricolpate, colpi frequently sinuous, irregular, 21–23 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire; tectate-perforate, wall relatively thin (ca. 1.5 μm); finely reticulate; 26–28 × 17–19 μm.

Eleven native species of *Dioscorea* are listed for Panama by Morton (1945), and Croat (1978) listed five native Central American species for Barro Colorado Island. *Dioscorea* is found primarily in the tropical moist, premontane moist, premontane wet, and tropical wet forests. *Rajania* is a West Indian segregate of *Dioscorea*. Similar pollen has been reported from the Miocene of Veracruz, Mexico (Graham, 1976).

EUPHORBIACEAE

Alchornea (Fig. 52). Oblate, amb circular; tricolpate, colpi straight, 6–8 μm long (pole to equator), equatorially arranged, meridionally elongated, equidistant, extending within 5–6 μm of pole, inner margin entire, distinct operculum; tectate, wall 1.5 μm thick; psilate to faintly scabrate; 20 μm.

Pollen of *Alchornea* is frequent in Gulf/Caribbean Tertiary deposits and ranges from the lower and middle Eocene (Colombia; González Guzmán,

1967) to Recent (Muller, 1981). Its distribution and ecology for the region have been summarized by Graham (1987a), based on Croat (1978) and Webster & Burch (1967). Briefly, it grows in the tropical moist, premontane wet, and premontane rain forest, with a wide altitudinal range of 300 to 2,000 m. Pollen of the family has been described by Punt (1962).

Sapium (Figs. 49, 50). Prolate; tricolporate, colpi straight, 62–66 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi 4–6 μm wide, margo present (formed by reticulum becoming finer bordering the colpi), pore large (12–14 μm diam.), oval, situated at midpoint of colpus; tectate-perforate, wall 3 μm thick, individual columellae distinct; finely reticulate; 76–80 × 52–56 μm.

Sapium is a genus of about 120 species (fide Willis, 1966) of trees and shrubs widely distributed in tropical and subtropical regions of the New World. Webster & Burch (1967) listed four species for Panama, and Croat (1978) recorded two for Barro Colorado Island. It grows in the tropical moist, premontane wet, and lower montane wet forests. Hartshorn (1983: 143–144) described its occurrence within the Monteverde Reserve in Costa Rica (cove, leeward cloud, windward cloud, and swamp forests).

There is considerable range in size of *Sapium* pollen, and the smaller forms (48 μm) have been described from the Quaternary of Panama (Bartlett & Barghoorn, 1973). Slightly larger specimens (58 μm) occur in the upper Miocene Paraje Solo Formation of Veracruz, Mexico (as cf. *Sapium*; Graham, 1976). The Culebra specimens are exceptionally large (80 μm) and are matched by a collection labeled *S. haematospermum* Muell.-Arg. (*Rocha 3666*, Argentina, TEX). It is not possible to refer the specimen to any one modern species, but pollen identical to the specimens in size and fineness of the reticulum apparently does occur in the genus.

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FIGURES 39–58. *Fossil pollen from the Culebra Formation, Panama.—39. Chenopodiaceae/Amaranthaceae. Pan core 470.6, slide 3a, ESF Q-39, 1.—40, 41.* Combretum/Terminalia. *Pan core 470.6, slide 2a, ESF O-16, 2–4; Pan core 456, slide 4, ESF W-15, 4.—42, 43.* Compositae. *Pan core 488, slide 1, ESF J-14, 4.—44, 45. Cf.* Rourea. *Pan core 456, slide 4, ESF T-32, 2–4; Pan core 456, slide 3, ESF W-23.—46–48. Cf.* Doliocarpus. *Pan core 469.8, slide 2, ESF K-23, 1–2; Pan core 456, slide 1, ESF L-26, 2–4.—49, 50.* Sapium. *Pan core 456, slide 4, ESF K-15; Pan core 456, slide 4, ESF G-12, 3.—51.* Dioscorea/Rajania *type. Pan core 470.6, slide 2a, ESF F-38, 3.—52.* Alchornea. *Pan core 469.8, slide 2, ESF T-15, 2–4.—53.* Casearia. *Pan core 470.6, slide 2a, ESF L-21.—54.* Acacia. *Pan core 488, slide 1, ESF R-34.—55–58.* Tetrorchidium. *Pan core 488, slide 1, ESF T-33, 2–4; Pan core 470.6, slide 2a, ESF Q-35, 2–4.*
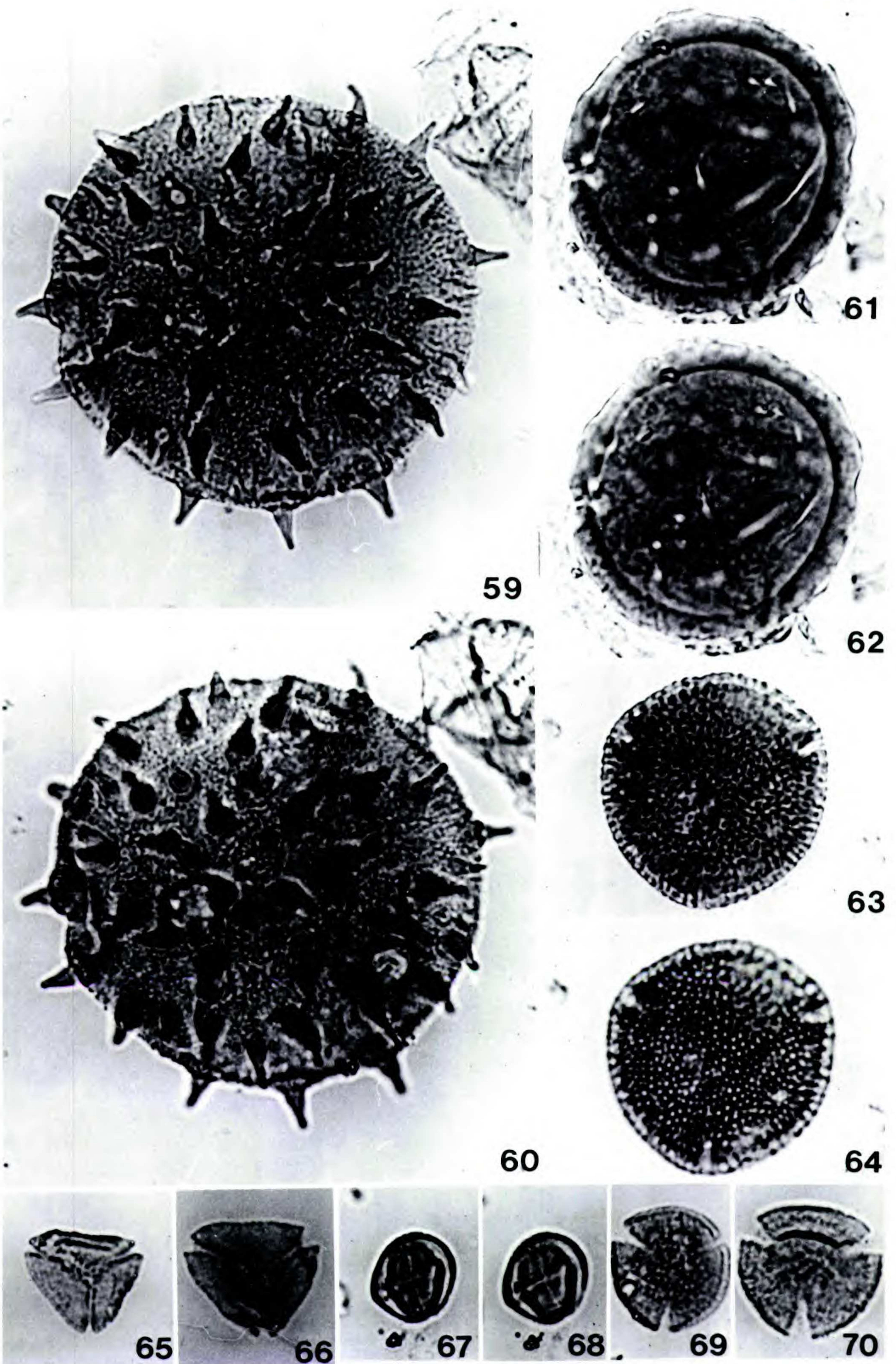
FIGURES 59–70. *Fossil pollen from the Culebra Formation, Panama.*—*59, 60. Hampea/Hibiscus. Pan core 488, slide 1, ESF C-29.—61, 62. Malpighiaceae. Pan core 488, slide 1, ESF B-26, 3.—63, 64. Sabicea. Pan*

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Tetrorchidium (Figs. 55–58). Oblate-spheroidal, amb circular; tricolpate, colpi straight, 12–14 µm long (pole to equator), equatorially arranged, meridionally elongated, equidistant, inner margin finely dentate; intectate, finely baculate to nearly echinate, wall ca. 1.5 µm thick; 26–30 µm.

According to Webster & Burch (1967), there are about ten species of *Tetrorchidium* in the New World (five in Africa), and two are listed for Panama (*T. euryphyllum* Standley, rainforests of Costa Rica and Panama; *T. gorgonae* Croizat). Hartshorn (1983) mentioned *Tetrorchidium* sp. in the swamp forests of the Monteverde Reserve in Costa Rica (associated with *Alchornea* and *Sapium*). Pollen wall thickness varies among the species of *Tetrorchidium*, and the specimens are similar to the thinner-walled forms in our collection (e.g., *T. rotundatum* Standley, Nicaragua). Similar pollen has been reported from the Oligocene of Puerto Rico (Graham & Jarzen, 1969) and the Miocene of Veracruz, Mexico (Graham, 1976).

FLACOURTIACEAE

Casearia (Fig. 53). Prolate; tricolporate, colpi straight, 18–20 µm long, apices acute, equatorially arranged, meridionally elongated, equidistant, inner margin entire, narrow costae colpi, pore equatorially elongated (colpi transversalis), 1.5–2 × 4–5 µm, situated at midpoint of colpus; tectate, wall 1.5 µm thick; sculpture subdued, appearing psilate; 23–25 × 16–18 µm.

Casearia pollen records in the Gulf/Caribbean Tertiary have recently been reviewed by Graham (1985). Briefly, it is known from the middle(?) to late Eocene (Gatuncillo Formation, Panama) to Recent. The modern plants are trees and shrubs widely distributed in tropical and subtropical regions, with eight species listed for Panama (Robyns, 1968). They are most typical of moist forest types but can range into somewhat drier habitats (Croat, 1978). Pollen of the family has been studied by Keating (1973).

LEGUMINOSAE–MIMOSOIDEAE

Acacia (Fig. 54). Solid sphere, 16-celled polyad, amb circular; nonaperturate; individual cells ± cubical, ca. 20 µm; tectate, wall 1.5 µm thick; faintly scabrate; 52–54 µm.

Woodson & Schery (1950b) listed 12 species of *Acacia* for Panama, and Croat (1978) recorded five for Barro Colorado Island. They grow mainly in the tropical moist forest (in contrast to the familiar savannah habitats of African and Australian species) but can range into drier vegetation types. *Acacia* pollen has been reported from the Oligocene San Sebastian Formation of Puerto Rico (Graham & Jarzen, 1969), and a similar grain was recovered from the Quaternary of Panama (as Mimosoideae; Bartlett & Barghoorn, 1973).

MALPIGHIACEAE

(Figs. 61, 62). Spherical, amb circular; periporate, pores circular, 4–5 µm diam., inner margin entire; tectate, wall thick (3–4 µm); scabrate; 38–42 µm.

Only two poorly preserved specimens of the Malpighiaceae were recovered from the Culebra Formation and serve only to record the family in the assemblage.

MALVACEAE

Hampea/Hibiscus (Figs. 59, 60). Spherical, amb circular; periporate, pores circular, 3–4 µm diam., inner margin entire, narrow annulus; tectate, wall 2 µm thick; echinate, spines 4–5 µm long, broadened at base, moderately dense (distance between spines ca. 6–8 µm); 48–70 µm.

Robyns (1964a) and Croat (1978) listed one species of *Hampea*, *H. appendiculata* (Donn. Sm.) Standley, for Panama and Barro Colorado Island. It is a shrub to mid-size tree growing in Honduras, Costa Rica, and Panama in the tropical moist, premontane moist, tropical wet, and premontane rain forests. *Hibiscus* is represented by 14 species in Panama (fide Robyns, 1965), and on Barro Colorado Island by three species (Croat, 1978). *Hibiscus sororius* L.f. is a herb to small suffrutex that is common in marshy areas as a component of floating masses of marshy and swamp vegetation (Croat, 1978: 583). Hartshorn (1983) listed it as a member of the coastal strand vegetation in Costa Rica. Although insect pollinated, with large (to 70 µm) echinate pollen, the plant grows in habitats that would be immediately marginal to the Culebra depositional basin, and fossil specimens are frequent in the deposits.

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core 470.6, slide 3a, ESF U-31, 3.—65, 66. Eugenia/Myrcia. Pan core 470.6, slide 3a, ESF Q-22, 4; Pan core 470.6, slide 3a, ESF D-26, 2–4.—67–70. Rhizophora. Pan core 456, slide 4, ESF J-17, 1; Pan core 456, slide 4, ESF Q-11, 3–4; Pan core 488, slide 1, ESF V-12, 3.

The *Hampea/Hibiscus* pollen type is recorded under the artificial generic name *Echiperiporites* and ranges globally from the upper Eocene to Recent. It is known from the upper Eocene of Venezuela (Muller, 1981), upper Miocene of Veracruz, Mexico (Graham, 1976), and the Quaternary of Panama (Bartlett & Barghoorn, 1973).

MYRTACEAE

Eugenia/Myrcia (Figs. 65, 66). Oblate; amb triangular; tricol(poroid)ate; colpi straight, 6–8 μm long (pole to equator), equatorially arranged, meridionally elongated, equidistant, inner margin entire, syncolpate, pores vaguely defined, located at apices of grain at midpoint of colpus; tectate, wall ca. 1.5 μm thick; scabrate; 12–16 μm.

Occurrences of *Eugenia/Myrcia* in the Gulf/Caribbean Tertiary have been discussed recently by Graham (1985, 1987a). It is frequent in the sediments, although not in high percentages, and ranges from the middle Eocene to Recent. Study of the modern pollen (Graham, 1980) indicates that isolated microfossils cannot be referred consistently to any one genus of the family, and the specimens serve only to document the Myrtaceae as a prominent component of the lower Miocene vegetation of Panama.

RHIZOPHORACEAE

Rhizophora (Figs. 67–70). Prolate to prolate-spheroidal; tricolporate, colpi straight, 14–16 μm, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 2–3 μm, pores elongated equatorially (colpi transversalis), 1 × 4 μm, constricted at midpoint of colpus; tectate-perforate, wall 2–3 μm thick; finely reticulate; 16–20 × 14–19 μm.

Records of *Rhizophora* pollen in the Gulf/Caribbean Tertiary have been summarized by Graham (1985: 519, 1987a). The Culebra specimens further document its widespread occurrence and often dominant percentages in sediments such as lignites deposited under warm-temperate to subtropical, coastal, brackish-water conditions. It ranges from late Eocene to Recent in tropical American sediments (often reported under the artificial generic name *Zonocostites*), and in older deposits is replaced by its presumed ecological counterpart, *Brevitricolpites* of unknown biological affinity. Other aspects of modern and fossil mangrove pollen have been discussed by Langenheim et al. (1967), Leopold (1969), and Muller & Caratini (1977).

RUBIACEAE

Sabicea (Figs. 63, 64). Oblate, amb oval-triangular to nearly circular; tricolpate/porate (apertures short, slitlike, ca. 2:1 length/width ratio), 4–6 × 2–3 μm, equatorially arranged, meridionally elongated, equidistant, inner margin faintly dentate (due to overlying sculpture elements), faint costae colpi; tectate-perforate, wall 2–3 μm thick; finely reticulate, muri smooth, width about same as diameter of lumen (ca. 0.5–1 μm); 32–36 μm.

The presence of *Sabicea* pollen in the Culebra assemblage has been reported recently by Graham (1988a). Briefly, the genus presently grows from Mexico to northern South America and is represented in Panama by three species and two varieties common in tropical moist and premontane wet forests. *Sabicea* has not been reported previously in the fossil record.

SAPINDACEAE

Allophylus (Figs. 71–75). Oblate to peroblate, amb distinctly triangular; triporate, pore slightly elongated meridionally, ca. 5 × 3 μm, equatorially arranged, equidistant, inner margin entire, faint costae colpi; tectate, wall 2 μm thick; scabrate to microreticulate; 14 × 24 μm.

Allophylus is a mostly South American genus of about 190 species of shrubs or small trees with six species in Mexico and Central America, and three in Panama (fide Croat, 1976). It typically grows at low to moderate elevations (ca. 1,000 m) and ranges through several forest types—tropical dry, tropical moist, tropical wet, premontane moist, and premontane wet forests. It has been reported previously from the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976).

Cupania (Fig. 76). Oblate to peroblate, amb triangular; tricolpor(oid)ate, colpi straight, 7–8 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, syncolpate; tectate, wall 2 μm thick; psilate to faintly scabrate; 12–16 μm.

Cupania is a genus of about 45 tropical American species of trees and shrubs. The nine species listed for Panama (Croat, 1976) grow primarily in the tropical moist, tropical wet, and premontane wet forests. The genus has been reported from the upper Miocene Paraje Solo Formation of Mexico (Graham, 1976) and from the Quaternary of Panama (Bartlett & Barghoorn, 1973).

Matayba (Fig. 77). Oblate, amb triangular;

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tricolpor(oid)ate; colpi straight, 12–14 μm long, apices branched with triangular sexine area included at poles, equatorially arranged, meridionally elongated, equidistant, inner margin entire; tectate, wall 2 μm thick; scabrate; 23–27 μm.

Croat (1976: 433) noted that *Matayba* is not always easily separable from *Cupania*. The pollen is also similar. *Matayba* pollen, however, commonly has branched colpi that include a triangular segment of the sexine at the poles, while in *Cupania* the colpi most frequently are unbranched or, when branched, do not usually include the triangular segment of sexine.

Matayba consists of about 45 species of trees and shrubs in tropical America, four of which are recorded for Panama (Croat, 1976), where it is found in the tropical dry, tropical moist, tropical wet, premontane moist, and premontane wet forests. *Matayba* has been reported from the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976).

SAPOTACEAE

Cf. *Pouteria* (Figs. 78, 79). Prolate; tricolporate, colpi straight, equatorially arranged, meridionally elongated, equidistant, inner margin entire, narrow costae colpi, pores elongated equatorially, 2–3 × 4–5 μm, situated at midpoint of colpus, narrow annulus; tectate, wall relatively thick (2–3 μm); faintly scabrate; 26–28 × 20–22 μm.

Pouteria is a genus of about 100 species of trees and shrubs found chiefly in tropical America. Included are a number of segregates that "are probably sound and deserve recognition at least at the subgeneric level. Unfortunately many of the segregate genera themselves are poorly defined, being based on relatively few specimens. As more material is collected, the generic limits may have to be shifted. This is particularly true among American species" (Pilz, 1981: 186).

The pollen is also similar to other members of the family, including *Sideroxylon*, which is a genus of trees and shrubs of the New and Old World tropics growing in Mexico, northern Central America, and Colombia but is not listed for Panama (Blackwell, 1968; Croat, 1978; D'Arcy, 1987). Species previously assigned to *Sideroxylon* from Panama are now mostly referred to *Pouteria* (e.g., *S. sapota* Jacq. = *P. sapota* (Jacq.) Moore & Stearn; *S. uniloculare* Donn. Smith = *P. unilocularis* (Donn. Smith) Baehni; Pilz, 1981). Collections at MO are rare from Mexico (one collection) and South America (two collections) but common from Asia, Africa, and Oceanica (Ricketson, pers. comm., 1987), suggesting a possible Old World origin. It is the only genus in the Culebra assemblage with this pattern of distribution, hence the provisional reference of the fossil specimens to *Pouteria*.

STERCULIACEAE

Cf. *Guazuma* (Fig. 80). Prolate; tricolporate, colpi straight, 16–18 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, narrow costae colpi, pores obscure, slitlike, ca. 1 × 3 μm, situated at midpoint of colpus; tectate-perforate, wall 2 μm thick; finely reticulate; 22–24 × 20–22 μm.

Guazuma is a genus of trees and shrubs consisting of three species with only *G. ulmifolia* Lam. listed for Panama (Robyns, 1964b). The latter species grows from Mexico to Panama and in the West Indies. It is ecologically variable and in Panama grows in the tropical moist, premontane wet, premontane moist, premontane dry, and tropical dry forests (Croat, 1978: 594).

UNKNOWNS

A number of specimens were recovered that could not be identified. Some of the more distinctive and/or abundant ones are illustrated and briefly described below.

Type 1 (Fig. 81). Spherical, amb circular; nonaperturate; intectate, wall thin (ca. 1.5 μm); echinate, spines short (ca. 2–3 μm), dense; 36 μm.

Type 2 (Figs. 82–86). Prolate; tri(?)colpate, colpi sinuous, 28–46 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire; tectate, wall 2–3 μm thick, homogeneous and hyaline; psilate to faintly textured (scabrate?); 32–50 × 19–34 μm.
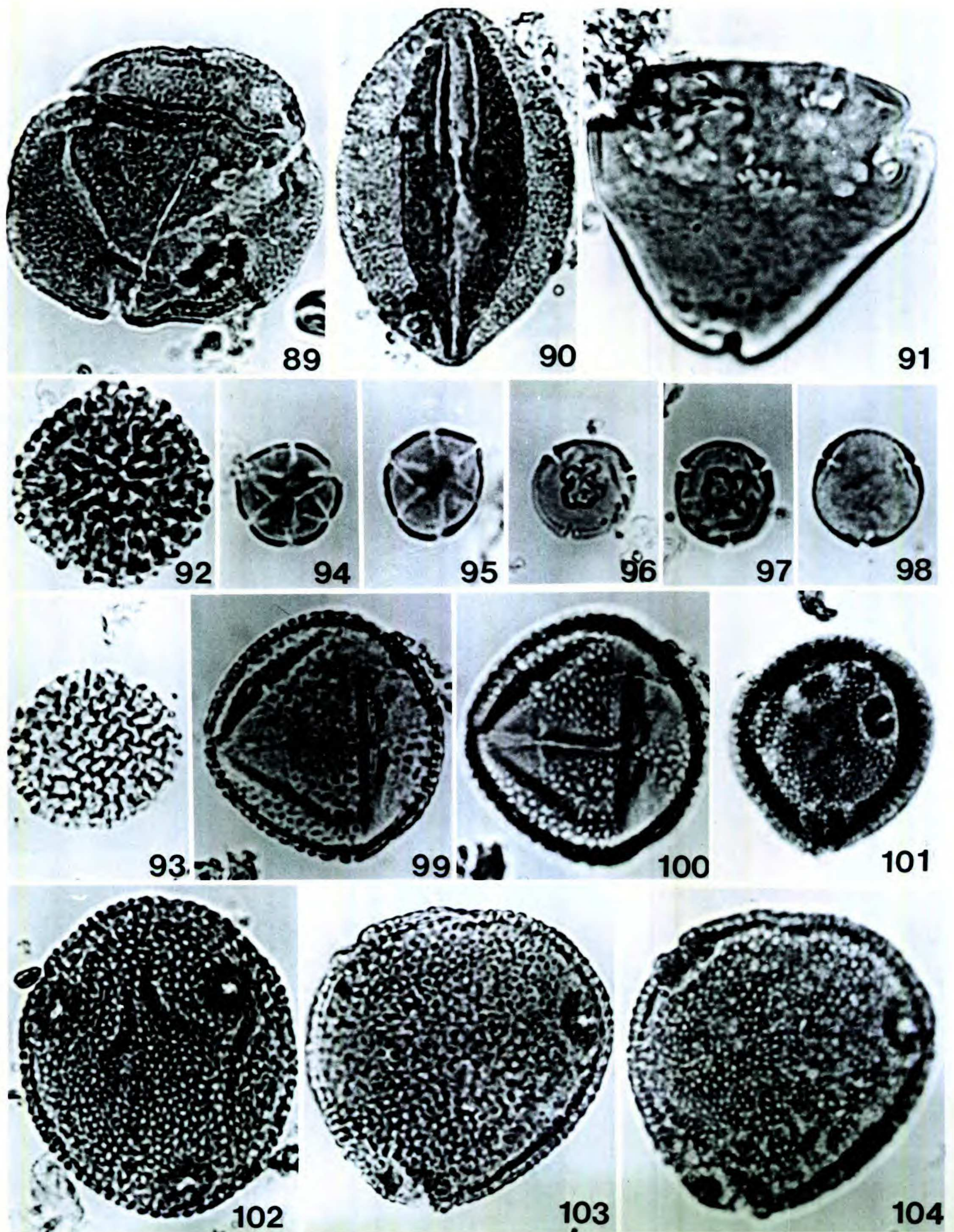
These specimens are characterized by a glass-like, hyaline wall and possibly represent an unknown fungal spore.

Type 3 (Figs. 87–90). Prolate; tricolporate, colpi straight, 40–46 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi 5–9 μm wide, pore slightly oval, 3 × 5 μm, situated at midpoint of colpus; tectate-perforate, wall 2 μm thick; finely reticulate; 42–55 × 32–43 μm.

These specimens are similar to pollen of several genera of the Anacardiaceae but also resemble
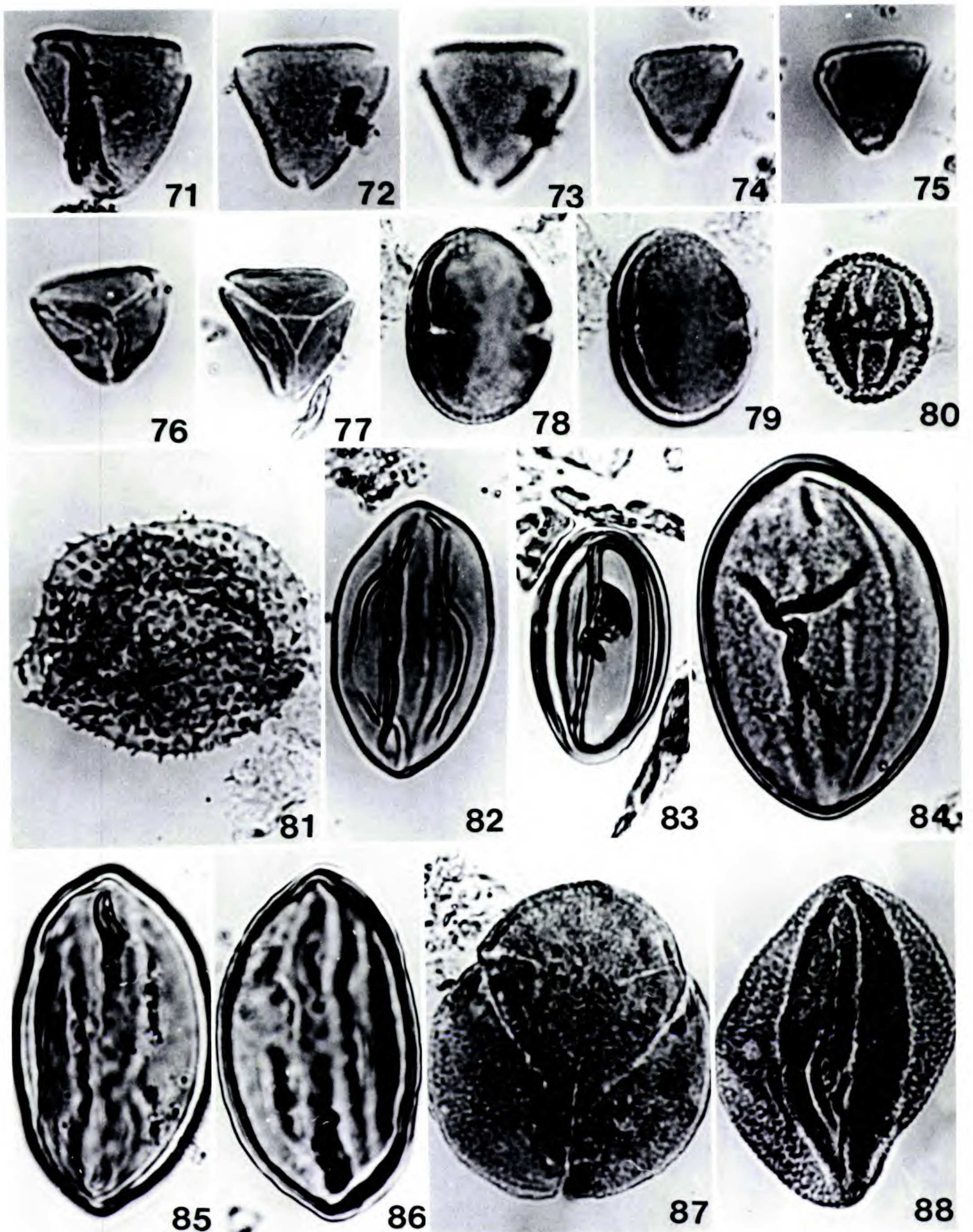
FIGURES 71–88. *Fossil pollen from the Culebra Formation, Panama.—71–75.* Allophylus. *Pan core 469.8, slide 1, ESF J-14, 1–3; Pan core 469.8, slide 2, ESF W-24, 2; Pan core 456, slide 3, ESF G-27, 1–3.—76.* Cupania. *Pan core 456, slide 3, ESF F-30.—77.* Matayba. *Pan core 470.6, slide 3a, ESF T-25, 2.—78, 79. Cf.* Pouteria. *Pan core 470.6, slide 3a, ESF J-35, 1–3.—80. Cf.* Guazuma. *Pan core 456, slide 4, ESF O-29, 4.— 81. Unknown type 1. Pan core 470.6, slide 3a, ESF Q-18, 4.—82–86. Unknown type 2. Pan core 490.6, slide 1, ESF Y-32, 1; Pan core 456, slide 1, ESF H-12, 4; Pan core 456, slide 3, ESF V-18, 4; Pan core 456, slide 1, ESF R-19, 3.—87, 88. Unknown type 3. Pan core 469.8, slide 1, ESF R-23, 1–2; Pan core 469.8, slide 1, ESF Q-30, 3–4.*

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FIGURES 89–104. *Fossil pollen from the Culebra Formation, Panama.*—*89, 90. Unknown type 3. Pan core 456, slide 1, ESF U-22, 1; Pan core 456, slide 3, ESF L-14, 2.—91. Unknown type 9. Pan core 456, slide 3, ESF R-26, 4.—92. Unknown type 14. Pan core 470.6, slide 3a, ESF F-36, 3–4.—93. Unknown type 13. Pan core 456, slide 1, ESF Q-37, 4.—94, 95. Unknown type 5. Pan core 456, slide 4, ESF F-17, 3–4; Pan core 456, slide 3, ESF P-25.—96–98. Unknown type 8. Pan core 456, slide 4, ESF K-30, 1; Pan core 456, slide 4, ESF P-25, 2–4.—99, 100. Unknown type 7. Pan core 469.8, slide 2, ESF U-25, 3–4.—101. Unknown type 12. Pan core 456, slide 4, ESF N-10.—102–104. Unknown type 11. Pan core 456, slide 3, ESF G-33; Pan core 488, slide 1, ESF V-27, 3.*

some Bignoniaceae and Euphorbiaceae. They are common in the Culebra assemblage and in several other Gulf/Caribbean Tertiary formations (e.g., Eocene Gatuncillo Formation, Panama; Graham, 1985, figs. 138–144).

Type 4 (Fig. 107). Oblate-spheroidal, amb circular; tetracolporate, colpi straight, equatorially arranged, meridionally elongated, equidistant, inner margin entire, pores equatorially elongated, ca. 1 × 4 μm, situated at midpoint of colpus; tectate, wall 2 μm thick; psilate to faintly scabrate; 23 μm.

Type 5 (Figs. 94, 95). Oblate to oblate-spheroidal; amb circular; stephanocolpate, colpi 6, straight, 6 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, pores equatorially elongated, ca. 1 × 4 μm, situated at midpoint of colpus; tectate, wall 2 μm thick; psilate; 14–16 μm.

Type 6 (Figs. 105, 106). Oblate-spheroidal, amb circular; tricolpor(oid)ate, colpi straight 15 μm long, equatorially arranged, meridionally elongated, equidistant, margin diffuse; tectate, wall 3 μm thick; scabrate, some sculpture elements more pointed, approaching echinae; 36 μm.

These specimens are generally similar to *Valeriana*, but no exact match could be found among the species examined.

Type 7 (Figs. 99, 100). Prolate-spheroidal; tricolpate, colpi straight, 22–24 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 3 μm wide, pores circular, 3 μm diam., situated at midpoint of colpus; tectate-perforate, wall 3 μm thick; reticulate, muri smooth, slightly narrower than the lumina; 36 μm.

These rare specimens may represent obliquely preserved specimens of *Coccoloba*.

Type 8 (Figs. 96–98). Oblate, amb spherical; tricolporate, colpi straight, short (4–6 μm), equatorially arranged, meridionally elongated, equidistant, inner margin entire, pores elongated equatorially (colpi transversalis), 1 × 5–6 μm, situated at midpoint of colpus; tectate, wall 1.5 μm thick; psilate to faintly scabrate; 14–20 μm.

Type 9 (Fig. 91). Oblate, amb triangular; tricolpate/porate (length/width ratio ca. 2:1), equatorially arranged, meridionally elongated, equidistant, inner margin entire, situated at apices of triangular grain; tectate, wall 2–3 μm thick; scabrate; 45 μm.

Type 10 (Fig. 108). Oblate to peroblate, amb oval-triangular to circular; tricolpate, colpi short

(3–4 μm), equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 3 μm wide; tectate-perforate, wall 2 μm thick; finely reticulate; 24–28 μm.

These specimens are similar to several Bombacaceae and related families (Tiliaceae, Sterculiaceae), but a precise identification could not be made.

Type 11 (Figs. 102–104). Oblate, amb circular; triporate, pores circular, 2–3 μm diam., equatorially to slightly subequatorially arranged (grains heteropolar), equidistant, inner margin entire, annulus 3–4 μm wide; tectate-perforate, wall 2 μm thick; finely reticulate; 43–50 μm.

These distinctive specimens are common in the Culebra Formation and probably represent a plant that was and likely still is common in the tropical American flora. The specimens are similar to *Bocconia arborea* S. Wats., but the modern pollen is periporate with only an occasional triporate grain, while the numerous specimens are all triporate.

Type 12 (Fig. 101). Oblate-spheroidal to spherical, amb circular; tri- to periporate, pores circular, 2 μm diam., conspicuous annulus 2–3 μm wide; tectate-perforate, wall thick (ca. 4 μm); finely reticulate; 35 μm.

Type 13 (Fig. 93). Spherical, amb circular; tricolpate (colpi short, obscure); tectate-perforate, wall thick (4–5 μm); reticulate, muri smooth, fine and slightly sinuous; 25–28 μm.

Type 14 (Fig. 92). These specimens are similar to Type 13, but the muri and walls are slightly thicker. Both are similar to pollen in some Rubiaceae (*Chomelia*, *Terebraria*) but do not match exactly any species in our reference collection.

In addition to these unknowns, there is also present the usual assortment of generalized small, prolate, tricolpate/colporate, finely reticulate forms common in Gulf/Caribbean Tertiary deposits. These are illustrated in Graham (1985, figs. 117–128). It is difficult to distinguish among these similar, intergrading types and they cannot presently be identified.

NUMERICAL REPRESENTATIONS

A total of 1,800 palynomorphs were tabulated from the Culebra material (200 each from levels 491.6–456, and 100 each from levels 425–377; Table 1). The ten most abundant types are as follows:

Monolete fern spore type 2: 367 specimens (20%)

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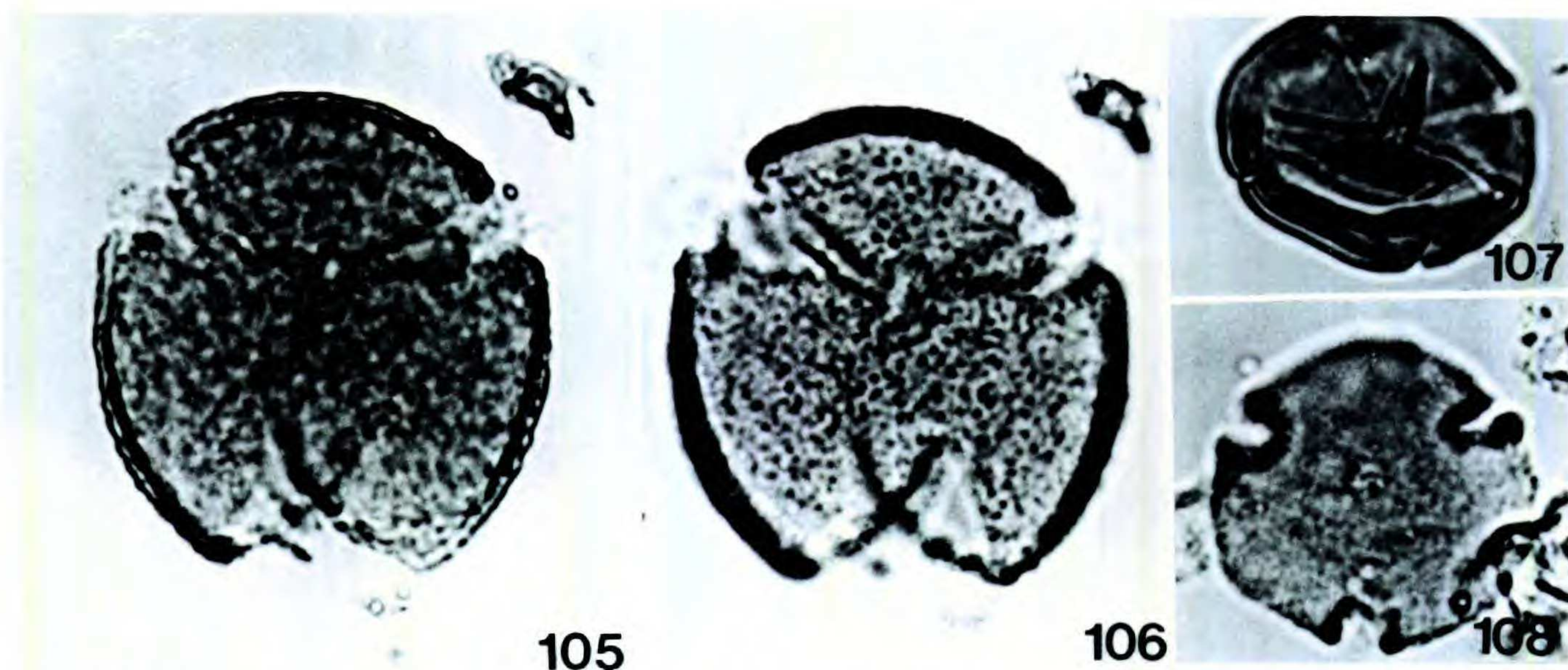
FIGURES 105–108.   *Fossil pollen from the Culebra Formation, Panama.—105, 106. Unknown type 6. Pan core 456, slide 3, ESF M-15, 3–4.—107. Unknown type 4. Pan core 488, slide 1, ESF J-13, 4.—108. Unknown type 10. Pan Core 456, slide 3, ESF F-25, 3.*

Manicaria-type palm pollen: 176 (10%)
Cyathea: 140 (8%)
Cryosophila-type palm pollen: 140 (8%)
Selaginella: 128 (7%)
Synechanthus-type palm pollen: 109 (6%)
Rhizophora: 100 (6%)
Monolete fern spore type 1: 84 (5%)
Hampea/Hibiscus: 68 (4%)
Lycopodium: 40 (2%)
Total ferns: 25%
Total cryptogams (ferns, *Lycopodium*, *Selaginella*): 40%
Total palms: 24%
Total lowland vegetation types (ferns, other cryptogams, palms, *Rhizophora*, *Hampea/Hibiscus*): 71%.

The composition of the Culebra flora clearly reflects a lowland tropical vegetation. Since the flora is derived from lignites deposited under lowland, coastal, brackish-water, warm-temperate to tropical conditions, there is a tendency to emphasize, possibly to over-emphasize, the potential bias toward this vegetation type. The actual bias is more in quantitative representation, with lowland communities over-represented and upland communities usually under-represented. Direct comparison of the fossil assemblage with modern vegetation types can be complicated further by differential preservation, insect versus wind pollination, and other factors. Thus attempts to quantify the paleocommunities in terms of relative abundance or aerial extent would be speculative, particularly in the absence of modern studies on pollen rain. Any impression, however, that major components of the vegetation, such as upland communities or savan-

nahs, are *a priori* missing from paleofloras derived from lignites is inconsistent with existing data. The middle to upper Oligocene San Sebastian flora of Puerto Rico (Graham & Jarzen, 1969) and the upper Miocene Paraje Solo of southeastern Mexico (Graham, 1976), both preserved in lignites, contain many representatives of inland and highland communities in the form of pollen and spores blown or washed into the lowland basins of deposition. The data show rather convincingly that virtually any tropical vegetation type can be represented in and recognized from palynofloras such as the Culebra. An exception may be paramo, since the pollen of some important components, such as Gramineae, Compositae, and Cyperaceae, cannot be differentiated from non-paramo species. In general, however, when the characteristic and defining members of a community are missing from a diverse and well-preserved palynoflora, this is likely due to the absence or poor representation of the community in the region rather than to an absolute bias in the depositional process.

Features traditionally examined in core material are the first and last appearances of distinct types, changes in percentages of individual types through the section, and similar data on groups or assemblages of types. The purpose is to assess the possibility of subdividing or zoning the section for more precise comparison with other sections or formations (stratigraphic correlation). Such analysis is difficult for the Culebra section because of the uneven quality of preservation along the core. For example, the lowermost (oldest) samples from 491.6 and 491 feet contain palynomorphs of only fair preservation and of low diversity (14 and 12 types of palynomorphs, respectively; Fig. 109). There
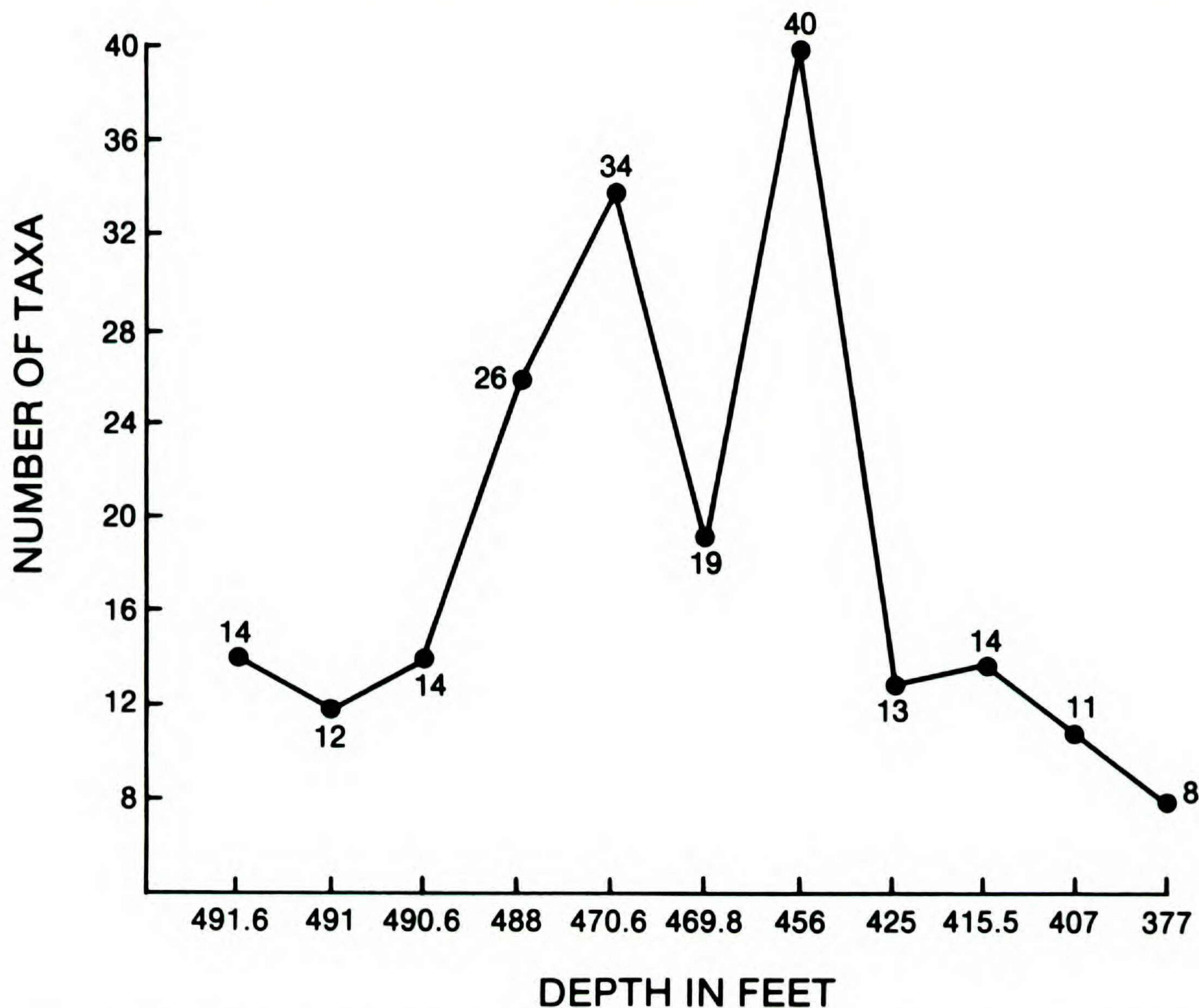
FIGURE 109. *Number of palynomorphs in each of the 11 samples from the Culebra core. Diversity and preservation were lowest at levels 491.6, 491, 490.6, 425, 415.5, 407, and 377, which also contained abundant fungal spores. Levels 470.6 and especially 456 contained the largest number of well-preserved palynomorphs and are probably most representative of the Culebra vegetation.*

are abundant thick-walled fern spores, suggesting possible differential preservation. Beginning with level 490.6, both the quality of preservation and diversity increase, which continue through level 456 (40 types), with the exception of a drop in diversity at level 469.8 (19 types). The remaining four samples (425, 415.5, 407, 377) are poor, with large numbers of thick-walled fern spores and fungal spores. It has been my experience in Gulf/ Caribbean Tertiary deposits that abundance of fungal spores usually coincides with a decrease in the quality, abundance, and diversity of pollen.

In light of the differences in preservation along the core, the facts that *Lycopodium* first appears at level 490.6, or *Pteris* and Malpighiaceae at level 488, probably do not carry much stratigraphic or paleoecological significance. In instances where a particular microfossil appears confined to a single level or narrow zone (e.g., *Desmoncus*-type, Che-

nopodiaceae/Armaranthaceae, Compositae, cf. *Doliocarpus, Alchornea, Casearia, Acacia, Eugenia/Myrcia, Sabicea*, cf. *Pouteria*, cf. *Guazuma*), the percentages are very low, and the zone is usually between levels 488 and 456, where diversity and preservation are generally high. One quantitative feature of the section that does appear real is the very high percentage of *Synechanthus*-type palm pollen at level 377. Not only are these grains numerically abundant, but many occur in dense, anther-size clusters, indicating that this layer likely was deposited under or immediately adjacent to a dense stand of these palms. Similar clusters of *Rhizophora, Pelliceria*, and monolete, verrucate fern spores (Polypodiaceae, Blechnaceae) occur in other Gulf/Caribbean Tertiary deposits.

Other than the unusual, and probably fortuitous, abundance of *Synechanthus*-type palm pollen at level 377, the quantitative features of the assem-

TABLE 2.   *Distribution of taxa identified from the lower Miocene Culebra Formation among comparable modern community types in Panama. Placement is according to principal or most common occurrence(s), and most range through more than one community.*

TROPICAL MOIST FOREST (30 genera)
    Lycopodium, Selaginella, cf. *Antrophyum, Cyathea, Danaea, Lygodium, Pteris, Cryosophila*-type, *Desmoncus*-type, *Manicaria*-type, *Synechanthus*-type, *Acacia, Alchornea, Allophylus, Casearia, Combretum, Cupania, Dioscorea,* cf. *Doliocarpus, Eugenia, Hampea, Matayba, Myrcia,* cf. *Pouteria, Rhizophora,* cf. *Rourea, Sabicea, Sapium, Terminalia, Tetrorchidium*

PREMONTANE WET FOREST (25 genera)
    Lycopodium, Selaginella, cf. *Anthophyum, Cyathea, Danaea, Lygodium, Pteris, Cryosophila*-type, *Manicaria*-type, *Synechanthus*-type, *Alchornea, Allophylus, Casearia, Combretum, Cupania, Dioscorea,* cf. *Doliocarpus, Eugenia,* cf. *Guazuma, Matayba,* cf. *Rourea, Sabicea, Sapium, Terminalia, Tetrorchidium*

TROPICAL WET FOREST (22 genera)
    Lycopodium, Selaginella, cf. *Antrophyum, Danaea, Lygodium, Pteris, Cryosophila*-type, *Desmoncus*-type, *Manicaria*-type, *Allophylus, Casearia, Combretum, Cupania, Dioscorea, Eugenia, Hampea, Hibiscus, Matayba, Myrcia,* cf. *Pouteria, Terminalia, Tetrorchidium*

PREMONTANE MOIST FOREST (12 genera)
    cf. *Antrophyum, Lygodium, Allophylus, Combretum, Dioscorea, Eugenia,* cf. *Guazuma, Hampea, Ilex, Matayba,* cf. *Rourea, Terminalia*

TROPICAL DRY FOREST (7 genera)
    Lygodium, Allophylus, Casearia, Combretum, cf. *Guazuma, Matayba,* cf. *Rourea*

LOWER MONTANE WET FOREST (6 genera)
    Lycopodium, Selaginella, Cyathea, Pteris, Manicaria-type, *Sapium*

LOWER MONTANE MOIST FOREST (5 genera)
    Lycopodium, Selaginella, Cyathea, Pteris, Manicaria-type

PREMONTANE RAIN FOREST (5 genera)
    Synechanthus-type, *Alchornea, Casearia, Hampea,* cf. *Pouteria*

PREMONTANE DRY FOREST (4 genera)
    Casearia, Combretum, Eugenia, cf. *Guazuma*

LOWER MONTANE RAIN FOREST (none)
MONTANE WET FOREST (none)
MONTANE RAIN FOREST (none)

blage do not suggest any distinct zones or significant change in vegetation other than the expected spatial reshuffling of local communities with minor changes in the landscape. The assemblage is best considered as a unit, with levels 488 to 456 most representative of the Culebra vegetation. The tabulations in Tables 1 and 2 provide the most complete listing presently available of plants and paleocommunities occurring on the volcanic islands constituting Central America ca. 20 Ma.

PALEOCOMMUNITIES

Genera identified from the Culebra Formation are arranged according to paleocommunities in Table 2. These are only approximations because the microfossils are mostly identifiable to genus, and many genera range through more than one community. On the other hand, recognition of the paleocommunities is based on the presence of characteristic genera and on the total number of genera indicative of a given assemblage rather than on single "key" members. Thus, the impact of any one assignment is reduced. Also, as data accumulate from other Tertiary fossil floras in northern Latin America, there is increasing consistency, both between floras and between the paleobotanical data and evidence derived from other independent lines of inquiry (see discussions in Graham, 1987a, b, 1988c, d) regarding the kinds of vegetation likely present in the Gulf/Caribbean region. As noted earlier, the prominent representation of wet- to moist-lowland communities, compared with higher-altitude and drier savannah-type vegetation, cannot be ascribed solely to bias in the depositional environment, because the latter communities are recorded in Gulf/Caribbean Cenozoic palynofloras.

Four paleocommunities are prominent in the Culebra flora (Table 2). The tropical moist forest is represented by 30 genera that presently occur in this community. Included is *Rhizophora*, establishing the presence of the mangrove swamp, although pollen was not abundant in this section. The maximum percentage was 10.5% at level 491.6, with an average of 5.8% for the 11 levels. This is in contrast to percentages as high as 96% in one sample from the Paraje Solo Formation of southeastern Mexico (Graham, 1976: 803, table 1). The absence of other mangrove genera such as *Avicennia, Conocarpus, Laguncularia,* and *Pelliceria* suggests: 1) the community was present but not dominant in the vicinity of the depositional basin at this time, and 2) that these sediments accumulated in an estuarian fern/palm marsh environment behind the mangrove zone. The record of *Rhizophora* can be quite variable through a section, however, reflecting changes in land/sea relationships in this tectonically active region. In January 1984, core material was received from another well drilled on the east bank of the Panama Canal just north of Gold Hill. The base of the core penetrated into the uppermost part of the Culebra Formation. The microfossils were similar to those from the core used in this study, but at level 171.65–171.9, near the transition between the Culebra and the overlying Cucaracha formations (slightly higher in the Culebra section than the material reported here), the assemblage was virtually 100% *Rhizophora*. These rapid changes in the abundance of mangrove pollen are useful in defining the position of former shorelines, and were used by Bartlett & Barghoorn (1973) to trace the history of Quaternary fluctuations in sea level in Panama. Mangrove vegetation was likely common throughout the Gulf/Caribbean region from the late Eocene onwards, even though its representation at a given locality varied with physiographic conditions.

The premontane wet forest potentially includes 25 genera, and the tropical wet forest 22 genera. Some form of the premontane moist forest (12 genera) was probably present, although the evidence is not as strong as for other lowland forests. Representation of vegetation types characteristic of higher altitudes and drier habitats (including savannahs) drops off significantly, and there is no palynological evidence for their presence. This is also true for the middle(?) to late Eocene Gatuncillo flora (Graham, 1985), and the Cucaracha (Graham, 1988b) and La Boca floras of Panama (Graham, in prep.).

Thus, the vegetation of the low-lying volcanic

islands constituting present-day southern Central America ca. 20 Ma consisted of a fringing zone of mangrove vegetation, with fern and palm swamps occupying the estuaries where fresh water diluted the brackish-water habitat of the mangroves. On adjacent, better-drained slopes were versions of the tropical wet, tropical moist, premontane wet, and premontane moist forests. Very local, edaphically controlled, temporal habitats supporting drier vegetation may have been present, but there is no paleobotanical evidence for these communities in the Culebra flora.

PALEOENVIRONMENTS

Of the 41 taxa recognized for the Culebra flora, all grow in southern Central America at present. The vegetation clearly grew under climatic conditions comparable to those presently prevailing in the coastal, lowland, and moderate-altitude habitats. It is not possible to quantify precisely the lower Miocene climates of the region, but the data from Barro Colorado Island cited by Croat (1978: 3–5) and from Costa Rica cited by Coen (1983) and Fleming (1986) provide approximations of the rainfall and temperature. For Barro Colorado Island, "Under the Köppen system of climatic classifications, BCI's climate is Am, or tropical Monsoon Climate. Annual rainfall on BCI ranges from 190 to 360 cm (76 to 143 inches); between 1924 and 1962 it averaged 275 cm (107.3 inches). This compares with an average 328 cm (128 inches) at Colón, on the Atlantic coast of the Canal Zone, and 177 cm (68 inches) at Balboa on the Pacific coast, during the same period" (Croat, 1978: 3; data from Rubinoff, 1974). The vegetation of the Culebra Formation is most similar to that of the present Atlantic coast of Panama. It is obvious that the existing climatic differentiation between a moist Atlantic side and a drier Pacific side did not prevail, at least to the same degree, in the lower Miocene when the present-day isthmus consisted of a series of islands. Regarding temperature, "The atmospheric temperature may vary from as low as 16.5°C (61.7°F) to as high as 35.5°C (95.9°F), with the lowest temperature being recorded within the forest during the rainy season and the highest at the Laboratory Clearing in the dry season. With rare exceptions the temperature ranges between 21 and 32°C (70° and 90°F) throughout the year, and the average ambient temperature in the Laboratory Clearing is 27°C (77°F). The seasonal variation in monthly averages is just 2.2°C" (Croat, 1978: 3).

Fleming (1986) presented similar rainfall data for ten sites in Costa Rica. Three of these form a

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transect from the Atlantic coast (site 10, Limón, elevation 5 m) up the Cordillera Central (site 8, Turrialba, elevation 602 m) to the Central Valley (site 6, San José, elevation 1,172 m). The mean annual rainfall is 353.6, 264.1, and 188.9 cm for the respective sites. These elevations and climatic conditions are considered similar to those prevailing on the islands of southern Central America during the lower Miocene. A generalized illustration of my concept of the spatial distribution of lower Miocene communities in southern Central America is shown in Wake (1987: 255, fig. 14), truncated at about 1,000–1,500 m elevation.

Estimates of general climate can be evaluated to some extent by comparison with ocean surface-water temperature curves derived from ^{18}O analysis of foraminifera and other marine invertebrates (Savin, 1977; Savin & Douglas, 1985; Savin et al., 1975). The curves have been discussed recently by Graham (1987b) in relation to emerging paleobotanical data for northern Latin America. The curve shows that during the lower Miocene temperatures were generally high, consistent with the tropical conditions suggested by the Culebra (Panama) and Uscari (Costa Rica) floras. A sharp drop occurred at the end of the Miocene, and this is clearly reflected in the composition and paleoecology of the late Miocene Paraje Solo flora of southeastern Mexico (Graham, 1976).

The affinities of the Culebra flora are distinctly Central and North American. There are no exclusively South American elements present, and those growing in South America are plants widespread throughout the neotropics (e.g., *Rhizophora*). This is the expected pattern of geographic affinity because the latest connection between the North and South American continents formed only in late Pliocene times, about 3 Ma (Stehli & Webb, 1985).

These data illustrate the consistency beginning to emerge between results from paleobotanical studies in the Neotropics and data derived from other independent sources. The paleoenvironmental reconstructions and biogeographic patterns, presently based on the Uscari and Culebra palynofloras, can be further evaluated and refined when studies on two additional lower Miocene floras are completed. These are the Cucaracha and La Boca floras from the Canal region of central Panama.

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